



# Native Earthworms of Australia II

(Megascolecidae, Acanthodrilinae)

G.R. Dyne & B.G.M. Jamieson

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## ABSTRACT

The present work describes the known Australian taxa (6 genera, 82 species and one subspecies) of the subfamily Acanthodrilinae of the family Megascolecidae. A major aim is to bring to light the manuscript species described by G.R. Dyne in a Ph. D. thesis (Dyne 1984) prepared under the supervision of the second author. The following genera, species and subspecies are described. Genus *Diplotrema* Spencer, 1900 (62 species, of which 33 are new, and two subspecies, of which one is new): *D. acropetra* Jamieson, 1997; *D. armatissima* Jamieson and Dyne, 1976; *D. armifera* sp. nov.; *D. athertoni* sp. nov.; *D. attenuata* Jamieson, 1997; *D. australis* (Michaelsen, 1889); *D. bidiverticulata* sp. nov.; *D. bifistularis* sp. nov.; *D. biloela* Blakemore, 1997; *D. boardmani* sp. nov.; *D. bulburrinensis* sp. nov.; *D. capella* Blakemore, 1997; *D. capricorniae* sp. nov.; *D. conwayi* sp. nov.; *D. cornigravei* (Michaelsen, 1907); *D. cornutheca* sp. nov.; *D. crateris* sp. nov.; *D. daemeli* (Michaelsen, 1910); *D. elstobi* Blakemore, 1997; *D. eremius* (Spencer, 1896); *D. eungellae* sp. nov.; *D. falcatoides* sp. nov.; *D. fragilis* Spencer, 1900; *D. glandifera* (Jamieson, 1995) new combination; *D. glareaphila* sp. nov.; *D. gracilis* sp. nov.; *D. helonoma* Dyne and Jamieson, 1998; *D. heteropora* Dyne, 1979a; *D. ingrami* sp. nov.; *D. inornata* sp. nov.; *D. insularis* Jamieson and Dyne, 1976; *D. intermedia* Jamieson and Dyne, 1976; *D. lamberti* sp. nov.; *D. longiductis* sp. nov.; *D. macleayi* (Fletcher, 1890); *D. magna* sp. nov.; *D. magnetis* sp. nov.; *D. mantoni* Jamieson and Dyne, 1976; *D. melaleucae* Jamieson and Dyne, 1976; *D. minuta* Jamieson and Dyne, 1976; *D. montislewisi* sp. nov.; *D. narayensis* Blakemore, 1997; *D. nemoralis* sp. nov.; *D. peraeintestinalis* sp. nov.; *D. planumfluvialis* Dyne, 1987; *D. proserpinensis* Dyne and Jamieson, 1995; *D. pseudospectabilis* sp. nov.; *D. quasifragilis* sp. nov.; *D. queenslandicus* (Michaelsen, 1910); *D. retractata* sp. nov.; *D. ridei ridei* Jamieson and Dyne, 1976; *D. ridei melvillensis* Jamieson and Dyne, 1976; *D. rigida* sp. nov.; *D. scheltingai* Jamieson, 1997; *D. schmardae* (Beddard, 1892) species dubium?; *D. shandi* Jamieson and Dyne, 1976; *D. socialis* Dyne, 1987; *D. spectabilis* sp. nov.; *D. spenceri* sp. nov.; *D. sulcata* sp. nov.; *D. tenuiseta* sp. nov.; *D. tyagarah* Dyne, 1979; *D. tyagarah carnarvoni* subsp. nov. Genus *Kayarmacia* Jamieson, 1997 (4 species, of which two are new): *K. adelphicus* Jamieson, 1997; *K. bursatus* sp. nov.; *K. cochlearis* sp. nov.; *K. queenslandicus* (Michaelsen, 1916). Genus *Microscolex* Rosa, 1887 (3 species): *M. dubius* (Fletcher, 1887) (circummundane); *M. macquariensis* (Beddard, 1896) (Macquarie Island); *M. phosphoreus* Dugès, 1837 (circummundane). Genus *Neodiplotrema* Dyne, 1997 (11 species): *N. ambrosensis* (Blakemore, 1997) new combination; *N. altanmoui* Jamieson, 1997; *N. deminutionis* Dyne, 1997; *N. exigua* Dyne, 1997; *N. lacisbrontoi* Dyne, 1997; *N. mcdonaldi* Jamieson, 1997; *N. occidentalis* Dyne, 1997; *N. paripunctata* Jamieson, 1997; *N. raveni* Dyne, 1997; *N. tumida* Dyne, 1997; *N. varionephrica* Dyne, 1997. Genus *Rhododrilus* Beddard, 1889 (1 species): *R. kermadecensis* Benham, 1905 (Tasmania and Kermadec Island). Genus *Torresiella* Dyne, 1997 (1 species): *T. singularis* Dyne, 1997. This study includes 178 illustrations. Evidence is reviewed supporting dismissal of the Acanthodrilidae and Octochaetidae *sensu* Gates (1959, 1972); the first was based on two symplesiomorphies (tubular prostates and holonephridia), the second on one symplesiomorphy (tubular prostates) and one highly homoplastic apomorphy (meronephridia).



## Introduction

The Australian representatives of the subfamily Megascolecinae of the family Megascolecidae were revised in a previous monograph (Jamieson 2000; see also, Supplement 2001). The present work revises the Australian taxa of the remaining subfamily, the Acanthodrilinae. A major aim of the work is to bring to light the manuscript species described by G.R. Dyne in a Ph.D. thesis (Dyne 1984) prepared under the supervision of the second author. A considerable portion of the material described formed part of the Jamieson collection, and was collected by successive research assistants or postgraduate students: E. Bradbury, A. Postle, T. Walker, R. Raven, W. Nash, on funding to BGMJ from the Australian Biological Resources Study and Australian Research Grants Committee. This monograph attempts to cover all known species, but considerable material remains to be examined, notably in the Jamieson Collection in the Queensland Museum.

The museums in which Australian Acanthodrilinae are lodged and the registration prefixes pertaining to these are as follows:

AM W	Australian Museum, Sydney
ANIC	National Insect Collection, Canberra
BM(NH)	Natural History Museum, London
HM V	Zoological Museum, Hamburg
MNH U	Zoological Museum, Humboldt University, Berlin
NMV G	Museum Victoria, Melbourne
NTM Wo	Northern Territory Museum, Darwin
TM K	Tasmanian Museum, Hobart
QM G, QM GH, QM LGH	Queensland Museum, Brisbane
USNM	United States National Museum, Smithsonian Institution, Washington DC
WAM P	Western Australian Museum, Perth

In a few cases, the type specimens of new species could not be located. In those situations we have, nevertheless, included the species by taking a wide interpretation of Art. 73.1.4., ICZN (1999):

*‘Designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation.’*

## Subphylum Euclitellata

Euclitellates (oligochaetes, branchiobdellidans and leeches) are hermaphrodite annelids which possess a clitellum, a modification of the epidermis that secretes the cocoon in which the eggs are deposited. It is located around and/or behind the female pores. This location of the clitellum contrasts with location anterior to the female pores in the only other annelids known to possess a clitellum, questid polychaetes (see Jamieson 1983a,b). Parapodia (seen in many polychaetes) are absent from all euclitellates. Setae, though they may be numerous, are never jointed and they are absent from leeches, other than *Acanthobdella* (the sister-taxon of the Euhirudinea), and from branchiobdellidans. Euclitellate sperm are distinctive in possessing a tubular structure (the acrosome tube) that supports the acrosome vesicle (Jamieson 2000).

## Class Oligochaeta

Oligochaetes are earthworms and their aquatic, marine and freshwater relatives. They are euclitellates with testes anterior to ovaries (the reverse of the arrangement in leeches). The basic genital arrangement may have been four gonadial segments, with two pairs of testes followed by two pairs of ovaries (the octogonadial condition). The acrosome tube is simple, lacking the anterior extension seen in Hirudinea; and the spermatozoal flagellum lacks the asymmetrical marginal fibre flanking the axoneme which occurs in branchiobdellids. Jaws, seen in branchiobdellidans and many leeches, are absent. The coelom is spacious, although somewhat restricted in some lumbriculids. Setae are rarely absent (*Achaeta* in the Enchytraeidae) whereas they are absent from all higher leeches. The basic number of setae is deduced to be four sets, possibly pairs, per segment. The prostomium is simple, never with paired sensory appendages (unlike polychaetes), though rarely (e.g. *Pristina* and *Stylaria* in the Tubificidae, Naidinae; some Glossoscolecidae) with a single median process. Posterior sucker-like structures are very rare (the enchytraeid *Aspidodrilus*) in contrast with their invariable presence, with restriction and fixation of segment numbers, in branchiobdellidans and leeches. Like all euclitellates, oligochaetes are hermaphrodite and insemination involves copulation (as in leeches but unlike most polychaetes, in which exceptions with copulation include the clitellate *Questa*). Spermatozoa are usually received in spermathecae. Fertilisation is only rarely internal (in Eudrilidae, possibly some Phreodrilidae) whereas in leeches it is always internal, by means of ectospermatophores or vaginal insemination). Ectospermatophores are uncommon in oligochaetes (Jamieson 2000).

## Subclass Crass clitellata Jamieson, 1988

Clitellum more than one cell thick.

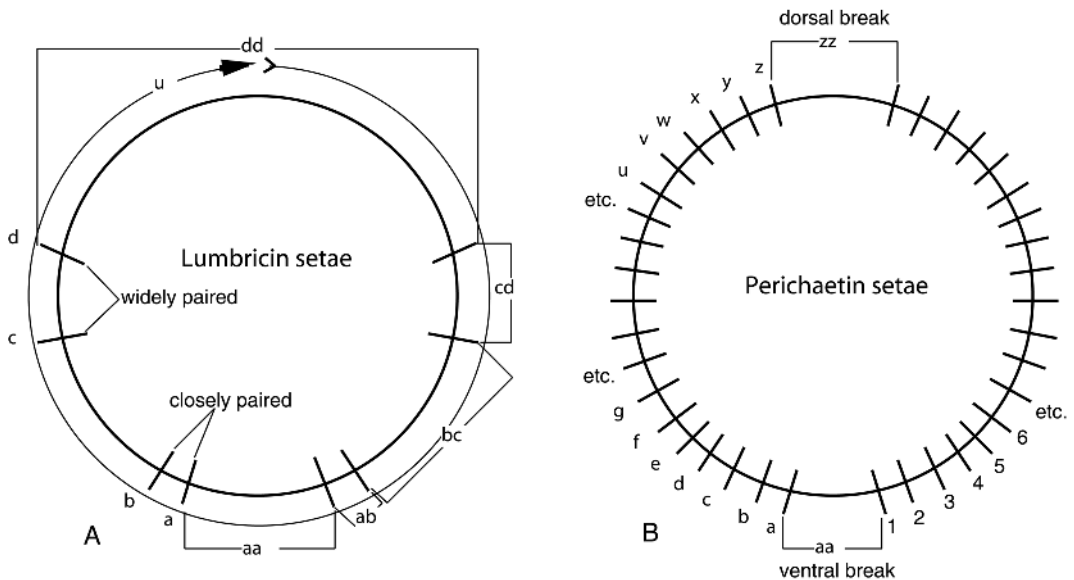
### REMARKS

The Crass clitellata was confirmed as monophyletic in a cladistic analysis of 28S rDNA sequences; the Megascolecidae were similarly shown to be monophyletic (Jamieson 2000; Jamieson *et al.* 2002).



## Family Megascolecidae Rosa, 1891 sensu Jamieson 2000, Jamieson *et al.* 2002

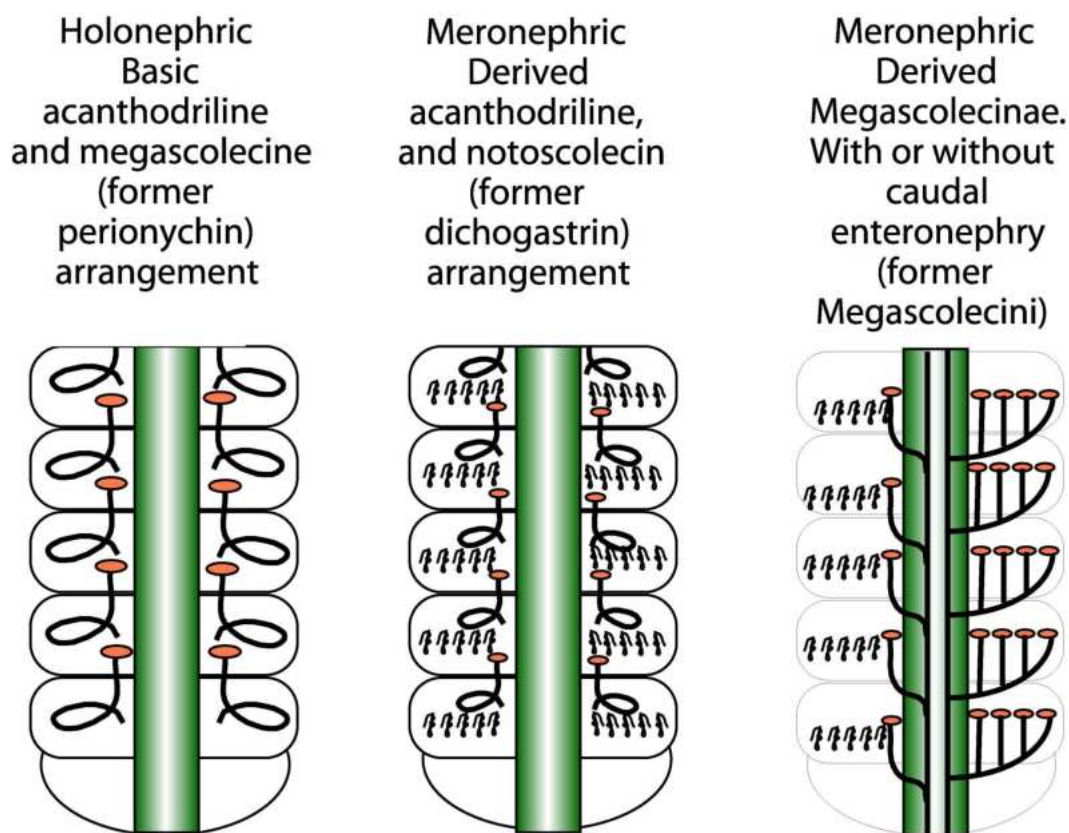
Small (ca 1 cm long) to giant (more than 2 metres long) earthworms. Setae usually four pairs per segment (the lumbricin condition, Fig. 1), sometimes six pairs, or more numerous, unpaired (the perichaetin condition, Fig. 1), to more than 100. Dorsal pores usually present. Male pores (openings of vasa deferentia) mostly on XVIII, or on XVII or XIX, or, rarely, one or two segments more posterior, or in XVI, paired, rarely single; exceptionally (*Hoplochaetella*) two pairs. If one pair on XVIII, united with the prostatic pores, or exceptionally (*Eudiplostrema*) separate. Prostatae one to three pairs; when two pairs, usually on XVII and XIX; when three pairs, in XVII, XVIII and XIX. Clitellum multilayered (the crassicitellate condition), saddle-shaped or, more usually, annular; on three or more of segments XII to XX. Female pores usually a pair on XIV, sometimes homeotically displaced; rarely two pairs, in XIII and XIV. Spermathecal pores pretesticular, usually paired, sometimes unpaired, rarely multiple per segment.



**Fig. 1.** The arrangement of setae in earthworms (Crassicitellata). The perichaetin condition is not seen in Australian acanthodrilids. They exhibit the lumbricin condition: eight setae per segment in four pairs, as seen in a transverse section of the body. The designation of setae as *a*, *b*, *c*, and *d* is shown together with intersetal distances (*aa* to *dd*) and the body circumference (*u*). [From Jamieson 2000]

Last hearts in XII or XIII, rarely if ever in the ocnodrilid location of XI. One to three oesophageal gizzards present, sometimes vestigial or absent. Intestinal gizzards and caeca rare. Extramural diverticula or calciferous glands frequently present; where present not arranged as in the Ocnodrilidae (not in IX or IX and X). Intestine commencing between XII and XX. Nephridia (Fig. 2) a pair per segment (holonephridia), or multiple per segment (meronephridia); some meronephridia may discharge into the foregut or intestine (enteronephry). Testes one or

two pairs, usually in X and XI; sometimes enclosed in testis-sacs. Ovaries in XIII (metagyny) or, rarely, in XII and XIII (hologyny); oocytes in several strings. Spermathecae usually paired and with one or more diverticula, sometimes unpaired, rarely adiverticulate.



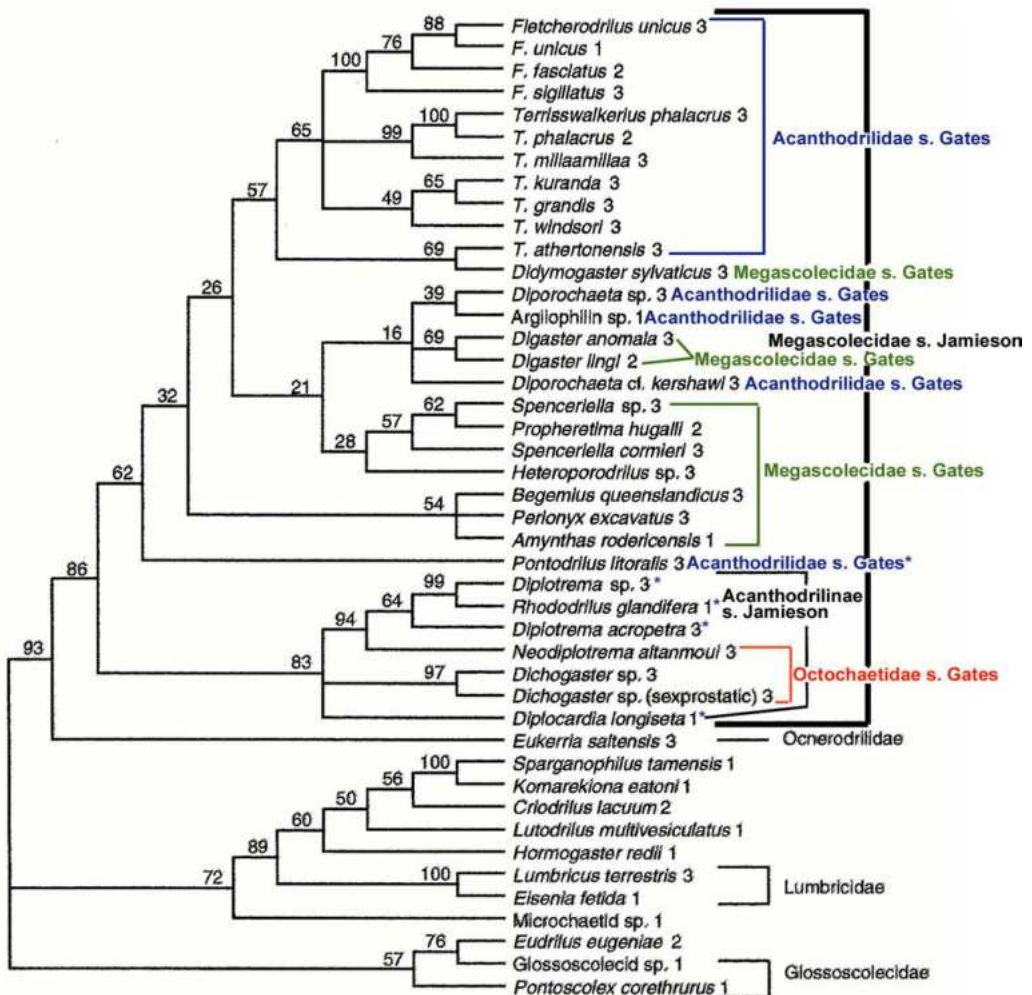
**Fig. 2.** Diagrammatic representation of types of nephridia in the Megascolecidae. The holonephric arrangement of one pair of stomate nephridia per segment occurs in most acanthodrilids; the meronephric arrangement, here with a median stomate meronephridium and lateral astomate meronephridia (micromeronephridia) is seen in *Neodiplotrema*.

[After Jamieson 2000]

## REMARKS

Analysis of megascolecoid oligochaete (earthworms and allies) nuclear 28S rDNA and mitochondrial 12S and 16S rDNA using parsimony and likelihood, partition support and likelihood ratio tests (Jamieson 2000; Jamieson *et al.* 2002), showed that all higher suprageneric classifications within the Megascolecidae were incompatible with the molecular data (Fig. 3). The results indicated that most of the suprageneric groupings were based on homoplasies, for instance, multiple origin of racemose prostates or of 'dichogastrin' meronephridia. The widely used classification (Gates 1972) of the non-ocnerodrilin Megascolecidae into three groups (Acanthodrilidae, with tubular prostates and holonephridia; Octochaetidae (see further discussion below), with tubular prostates and meronephridia; and Megascolecidae, with racemose prostates) was not supported by molecular data. Moreover, the subdivisions Perionychini, Dichogastrini and Megascolecini of the Megascolecinae (Jamieson 1971a-c) were

shown to be grades rather than clades. Division of the Megascolecidae *sensu stricto* into the subfamilies Megascolecinae and Acanthodrilinae was upheld, but taxa with the acanthodrilin arrangement of male pores and meronephridia formerly placed in the Dichogastrini were shown to be referable to the Acanthodrilinae. Exclusion of ocnodrilids as a sister-family of the Megascolecidae was supported. Suprageneric (tribal) divisions of the Megascolecinae, and Acanthodrilinae, are not therefore recognised here pending further analyses.



**Fig. 3.** Phylogeny of major earthworm (crassieitellate) families based on analysis of combined 28S, 12S and 16S sequences: 1, 28S (12S only for *Diploptrema glandifera* (Jamieson, 1995)); 2, 28S + 12S; 3, 28S + 12S + 16S. Note that the phylogram indicates that the microscoclec *Rhododrilus glandifera* (Acanthodrilinae) lies within the *Diploptrema* clade. [Relabelled after Jamieson *et al.* 2002]

## **Subfamily Megascolecinae** **sensu Jamieson 2000, Jamieson *et al.* 2002**

Male terminalia with only one pair of prostates, the pores of which are near to or combined with the male pores (openings of vasa deferentia) on XVIII or its homeotic equivalent. Genital pores sometimes unpaired, midventral. Prostates tubular, tubuloracemose or racemose. Purely holonephric or meronephric, or with meronephridia in a varying number of segments anterior to holonephridia.

### **DISTRIBUTION**

PALAEARCTIC: China, Korea, Japan. NEARCTIC: N America. NEOTROPICAL. ORIENTAL: India; Pakistan and northwards beyond Nepal; Sri Lanka; Assam; Burma; Java; Sumatra; Philippines; Moluccas. AUSTRALIAN: Australia including Tasmania; Norfolk Island; New Guinea. NEW CALEDONIA. NEW ZEALAND and neighbouring Islands including Chatham Island. Some species peregrine, sometimes widely.

## **Subfamily Acanthodrilinae** **Vejdovsky, 1884, *sensu* Jamieson, 2000, Jamieson *et al.* 2002**

Setae usually four pairs per segment, sometimes more numerous. Calciferous glands, often absent. Last hearts in XII or XIII. Male pores usually on XVIII, sometimes shifted posteriorly onto XIX, XX or XXI, rarely in XVI. Prostatic pores two pairs on the segments anterior to and posterior to the male pore segment (acanthodrilin arrangement), or one pair on the segment anterior to that of the male pores (microscolecine arrangement) or on the segment behind that of the male pores (balantin arrangement); in microscolecine and balantin species the male and prostatic pores may open on the same segment, or even by a common atrium. Sometimes (*Pickfordia*, part., *Dichogaster*, type-species) with three pairs of prostatic pores, in which case one pair lies in or near the male pore segment and may be united with the male pores; prostates never united with the male pores on XVIII even if only a single pair of prostates (unlike Megascolecinae). Genital pores sometimes unpaired, midventral. Prostates tubular, or rarely (*Exxus*, some *Diplotrema*) two pairs of tubuloracemose prostates in the acanthodrilin arrangement. Nephridia holonephridia, mixed holonephridia and meronephridia or meronephridia only; with or without terminal bladders. Gizzard oesophageal, usually one, sometimes two or three, anterior to the testis segments; sometimes poorly muscularised or absent. Intestine beginning in or behind XIV. Testes two pairs in X and XI (holandric arrangement) or one pair in X (proandric arrangement), or one pair in XI (metandric arrangement). Spermathecal pores in acanthodrilin species two pairs or a midventral pore, at intersegments 7/8 and 8/9, rarely in addition at one or more of the adjacent intersegments; in microscolecine species, one pair at 7/8 or 8/9, rarely absent.

### **DISTRIBUTION**

NEARCTIC: southern N America; Mexico (Amecameca). NEOTROPICAL: Mexico (Yucatan); Chile; Tierra del Fuego; Fuegian Archipelago; Falkland IIs; Central America and Caribbean Region. ETHIOPIAN: holonephric genera in S Africa; meronephric genera (e.g. *Dichogaster*) in tropical and subtropical regions. FIJI. MALAGASIAN: Madagascar. ORIENTAL. AUSTRALIA. NEW ZEALAND and offshore islands. SUBANTARCTIC ISLANDS.

## REMARKS

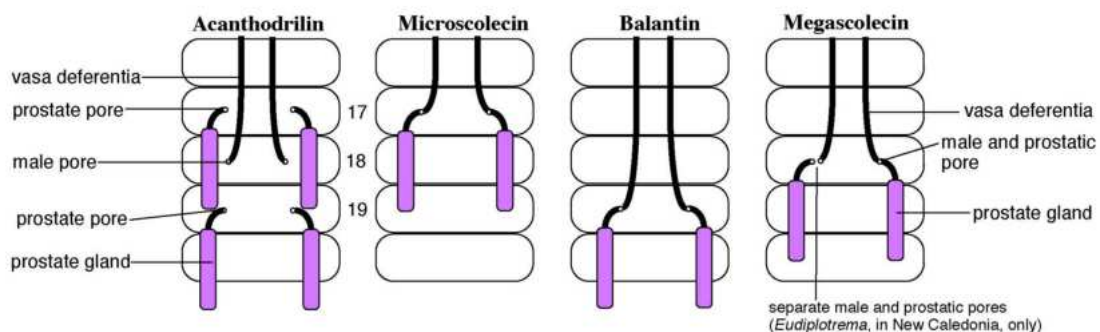
The above definition of the Acanthodrilinae is modified from Pickford (1937) and Jamieson (1971a,b) and accords with the generic constitution of the subfamily recognised on the basis of analysis of 28S + mitochondrial 12S +16S rDNA sequences by Jamieson (2000) and Jamieson *et al.* (2002). Pickford did not, however, include meronephric species. These she placed in the now obsolete Octochaetinae. Meronephric forms, including the former Octochaetidae, were included in the Acanthodrilinae by Lee (1959), on morphological grounds, and by Jamieson (2000) and Jamieson *et al.* (2002) on the basis of the molecular evidence. Lee, however, included all members of the Ocnerodrilidae in the Acanthodrilinae whereas the Ocnerodrilidae is shown from molecular evidence to be the sister-taxon of the Megascolecidae, consisting of the Megascolecinae and Acanthodrilinae (Jamieson 2000; Jamieson *et al.* 2002).

**Rejection of Acanthodrilidae *sensu* Gates.** The emendment of the Acanthodrilidae by Gates (1959, 1972) to include all non-ocnerodriles with tubular prostates and holonephridia has previously been refuted (Jamieson 1971a, 2000, 2001; Jamieson *et al.* 2002); the two defining characters were symplesiomorphies. Molecular analysis (Fig. 3) showed that *Fletcherodrilus*, *Terrisswalkerius*, *Diporochaeta*, an argilophilin species and *Pontodrilus*, all of which have tubular prostates, and are Acanthodrilidae *sensu* Gates, are dispersed among genera with racemose prostates in a clade representing the Megascolecinae. This clade is cladistically distinct from the Acanthodrilinae represented by *Diploptrema* and *Diplocardia* (Acanthodrilidae *sensu* Gates), and *Neodiploptrema* and *Dichogaster* (Octochaetidae *sensu* Gates).

**Rejection of Octochaetidae *sensu* Gates.** The grouping Octochaetidae *sensu* Gates (1959) has also been unequivocally refuted (Jamieson 1971a, 2000, 2001; Jamieson *et al.* 2002), being defined on only two characters: the symplesiomorphy of tubular prostates and the highly homoplastic apomorphy of meronephridia. On phylogenetic grounds the meronephric condition of the Octochaetidae(-inae) might be suspected to represent a grade rather than a single clade. It is therefore noteworthy that from morphological and zoogeographical considerations, and before the advent of the molecular studies referred to above, Lee (1959) concluded convincingly that some meronephric New Zealand worms (Octochaetidae *sensu* Gates) were derived locally (and convergently, i.e. homoplastically) from holonephric genera of the Acanthodrilinae. The pairs of meronephric and holonephric genera which he recognised were: *Octochaetus* and *Eodrilus*; *Deinodrilus* and *Eudinodriloides* (or *Dinodriloides*); *Hoplochaetina* and *Perieodrilus*; and *Leucodrilus* and *Rhododrilus*. Similarly, in northeastern Australia, the meronephric *Neodiploptrema* (see that genus below) appears to be derived from holonephric species attributable to *Diploptrema*.

In the highly objective, though phenetic, computer analysis of morphological resemblance by Sims (1966), we see the validity of Lee's suggestion of affinity of meronephric with holonephric genera largely confirmed, albeit not in precisely the pairs noted by Lee, though Sims endorsed recognition of the Octochaetidae. Thus *Octochaetus* (*O. paliensis*, assignable now to the Indian *Octochaetona*) was the 'nearest neighbour' of *Rhododrilus* and the highest coefficient of resemblance of *Deinodrilus* was with *Acanthodrilus*, that of *Perieodrilus* was equal with *Acanthodrilus* and *Deinodrilus*, and that of *Leucodrilus* was with *Acanthodrilus*.

Lee (1970), re-examined the affinities of the meronephric New Zealand species, also using computer techniques, and demonstrated the following affinities with holonephric genera for the meronephric genera discussed above: 1, the meronephric genera *Deinodrilus*, *Hoplochaetina*, *Octochaetus* (including their type-species) clustered with the holonephric



**Fig. 4.** The chief arrangements of prostatic and male pores in the Megascolecidae, Megascolecinae and Acanthodrilinae. [From Jamieson 2001]

'*Eodrilus*' (part., excluding the type-species, which was not considered); 2, *Leucodrilus* (meronephric), *Microscolex* (holonephric) and *Rhododrilus* (holonephric, including the type-species, and one mixed holonephric and meronephric species) formed a cluster.

These results confirmed the close relationship between meronephric and holonephric genera revealed by Lee (1959) and, though not considered significant, by Sims (1966) and endorsed by molecular evidence (Jamieson 2000; Jamieson *et al.* 2002). Thus, the holonephric *Diploplema* and *Diplocardia* (Acanthodrilidae *sensu* Gates) form a clade with the meronephric *Neodiploplema* and *Dichogaster* (Octochaetidae *sensu* Gates), in the Acanthodrilinae *sensu* Jamieson (Fig. 3). Further molecular studies should include the pairs of holonephric and meronephric genera recognised by Lee (1959, 1970). The Octochaetidae *sensu* Gates, and of recent attempts to resurrect it, is cladistically invalid.

**Relationships of some acanthodrilid genera.** Continuing molecular studies will be essential for resolution of relationships among the acanthodrilid species and delimitation of supra-specific, including generic, groupings. It is unlikely, when a more comprehensive molecular analysis has been made, that the present number, and definition, of acanthodrilid genera, or, indeed, any conventional Linnaean ranks, will adequately express their interrelationships. Most of these genera are at present defined by their different permutations of a small set of morphological characters, and some discussion of the genera relevant to the Australian Acanthodrilinae is appropriate here and under each genus.

The pivotal genus in determination of relationships and appropriate taxonomic nomenclature is the type-genus of the Acanthodrilinae, *Acanthodrilus*. *Acanthodrilus* Perrier, 1872, takes priority over *Microscolex* Rosa, 1887, *Diplocardia* Garman, 1888, *Notiodrilus* Michaelsen, 1899, and *Diploplema* Spencer, 1900, respectively, to cite the main genera with which we are concerned. As noted by Jamieson and Bennett (1979), the presence in *Acanthodrilus* (chiefly New Caledonia) of genital setae, in the vicinity of the spermathecae, which are often indistinguishable from those of *Diploplema* (Australia) indicates, with general morphological similarity, that the two entities are closely related, and, as a whole, *Acanthodrilus* is distinguished only by presence of nephridial vesicles. Similar setae occur in the digastric North American genus *Diplocardia* which Jamieson and Dyne (1976) maintain is also closely related to *Diploplema*, despite assertions of Gates (1977) to the contrary. They

also occur in one species of the derivative Australian genus *Kayarmacia*. The peculiar scalloped ornamentation of the setae in all of these genera militates against their convergent acquisition. Molecular phylogeny (Fig. 3) and morphological considerations suggest that spermathecal genital setae may be a synapomorphy for the clade containing these genera and that where they are absent, as in a few species of *Diploptrema* and *Dichogaster*, this represents a loss. It is noteworthy that of two Mexican species assigned to *Diploptrema* one has spermathecal genital setae, though these differ in ornamentation from those of Australian species. Fragoso and Rojas (1994) have reasonably assigned them to a distinct genus, *Kaxdrilus*. Molecular studies would, nevertheless, be desirable to ascertain the degree of relationship of the Mexican species to *Diploptrema* in Australia. *Diplocardia* was regarded by Jamieson and Bennett (1979) as the apomorphic sister-group of *Diploptrema*, being distinguished from the latter by duplication of the gizzard. However, although *Diplocardia* is undoubtedly close, *Acanthodrilus* and *Diploptrema* appear to be sister-taxa vicariated by tectonic separation of New Caledonia from Australia.

The various acanthodrilid genera appear to represent geographically distinct portions of a Gondwanan acanthodrilid fauna and *Diplocardia* may indicate a Mesozoic incursion into Laurasia. Such genera as the Australian *Kayarmacia* appear to represent further radiation within continental boundaries after tectonic breakup of Gondwanaland.

**Male genital pore arrangements.** The chief arrangements of prostatic and male pores in the Megascolecidae (Megascolecinae and Acanthodrilinae) are illustrated in Fig. 4.

In the acanthodrilin arrangement, there is a pair of prostatic pores in each of segments XVII and XIX with the male pores in XVIII. In the New Caledonian genus, *Acanthodrilus*, the pores may be displaced one or two segments posteriorly (Jamieson and Bennett 1979). The acanthodrilin arrangement is predominant in Australian Acanthodrilinae.

The microscolecin condition (Fig. 4) in which there is a single pair of prostatic pores on XVII opening with or near the male pores has been acquired in several Australian Acanthodrilinae and, it is deduced, this has occurred independently at least twice and probably more frequently. The evidence from extra-Australian species, such as *Notiodrilus georgianus* (see Pickford 1932) in which the acanthodrilin and megascolecic conditions can occur intraspecifically, is that the microscolecin condition has originated from the acanthodrilin condition (Fig. 4) by loss of the posterior prostates and migration of the male pores towards the remaining prostatic pores on segment XVII, as argued by Michaelsen long ago. *Neodiploptrema lacisbronti* shows what appears to be a transitional condition between the two states as, though it is acanthodrilin in having two pairs of prostates, the male pores are near intersegment 17/18. This condition has been taken further, independently, in *Diploptrema pseudospectabilis*, in which there is a single pair of prostates in XVII but the male pores have reached only intersegment 17/18.

The microscolecin Australian acanthodrilids are *Diploptrema glandifera* (Jamieson, 1995), new combination; *Diploptrema pseudospectabilis* sp. nov.; *D. retractata* sp. nov.; *D. gracilis* sp. nov.; *Kayarmacia adelphicus* Jamieson, 1997; *K. bursatus* sp. nov.; *K. cochlearis* sp. nov.; *K. queenslandicus* (Michaelsen, 1916); and *Rhododrilus kermadecensis* Benham, 1905.

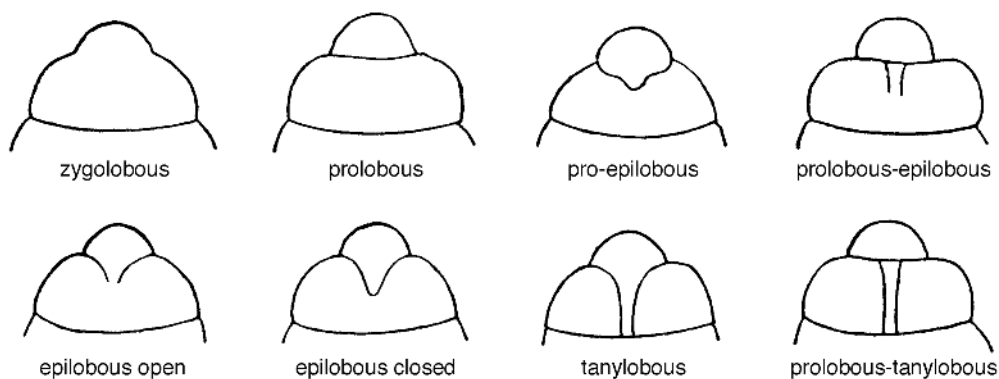
Dyne (1984) noted that it was tempting to place *Diploptrema pseudospectabilis*, *D. retractata* and material here referred to *D. glandifera*, in the heterogeneous microscolecin New Zealand genus *Rhododrilus*, but he recognised their obvious affinities with geographically close acanthodrilin species of *Diploptrema*. Analysis of 28S rDNA sequences (Fig. 3) confirmed placement of *D. glandifera* (there under the name *Rhododrilus glandifera*) in the *Diploptrema* clade.

Dyne observed, however, that there remained a small nucleus of Australian ?*Rhododrilus* species that appeared to have no close relatives in *Diploptrema* or *Neodiploptrema*. Their isolated position was emphasised by the mutual possession of the spermathecal pores in 7/8, rather than in the usual microscolecin reduction position of 8/9, and obvious fusion of the vasa deferentia and prostatic ducts to form a common duct that is conspicuously dilated. The latter arrangement is distinct from that found in the other Australian microscolecin taxa in which the openings of the male and prostatic ducts are merely approximated at the exterior, with no apparent internal conjunction. He considered that both of the anatomical features mentioned above would appear to point to a longer microscolecin history for these forms, as opposed to the comparatively more 'recent' reductions suspected for the above mentioned microscolecin *Diploptrema* species. These included, in addition to two apparent *nomina dubia*, *R. queenslandicus* and a species here tentatively referred to *Diploptrema*, *D. gracilis*. *R. queenslandicus* was placed independently in a separate genus, *Kayarmacia*, with *Kayarmacia adelphicus* Jamieson as its type-species, by Jamieson (1997). The two other similarly characterised new species which Dyne had reluctantly placed in *Rhododrilus* are also placed here in *Kayarmacia*, *K. bursatus* and *K. cochlearis*.

In the present work only a single Australian species is referred to *Rhododrilus*, namely *Rhododrilus kermadecensis* Benham, 1905, and this is a euryhaline subantarctic species not to be considered an Australian endemic. *Rhododrilus*, a predominantly New Zealand genus, is clearly polyphyletic and is diagnosed by the microscolecin condition and large gizzard.

Only *Torresiella singularis* Dyne, 1997, is known to have the balantin condition (a pair of prostates and male pores in segment XIX; see Fig. 4) in Australia.

The megascolecin condition, in which male and prostatic pores open in common or close to each other on segment XVIII is not seen in Acanthodrilinae. A *lapsus* in Jamieson *et al.* (2002) stated that the prostates discharge in XVIII in *Rhododrilus*; rarely the male pores, but not the prostates, may open on XVIII in that genus.



**Fig. 5.** Types of prostomia in earthworms.

[From Jamiesons 2000, after Michaelsen]



## LIST OF GENERA OF ACANTHODRILINAE IN AUSTRALIA

*Diploptrema* Spencer, 1900  
*Kayarmacia* Jamieson, 1997  
*Microscolex* Rosa, 1887

*Neodiploptrema* Dyne, 1997  
*Rhododrilus* Beddard, 1889  
*Torresiella* Dyne, 1997

## KEY TO GENERA OF ACANTHODRILINAE IN AUSTRALIA

(Applicable only to Australian taxa)

- 1 a. Prostatic pores 2 pairs, in segment XVII and XIX ..... 2
- b. Prostatic pores 1 pair, in segment XVII or XIX ..... 4
- 2(1a) a. Holonephric ..... 3
- b. Meronephric ..... *Neodiploptrema* (part.)
- 3(2a) a. Nephridial bladders present ..... *Microscolex* (part. — *M. macquariensis*)
- b. Nephridial bladders absent. .... *Diploptrema* (part.)
- 4(1b) a. Prostatic pores in XVII only ..... 5
- b. Prostatic pores in XIX, combined with the male pores. .... *Torresiella*
- 5(4a) a. Spermathecae 3 pairs ..... *Rhododrilus* (part. — *R. kermadecensis*)
- b. Spermathecae 1 pair or absent ..... 6
- 6(5b) a. Nephridial bladders absent. Spermathecae 1 pair .....
- b. Nephridial bladders present. Spermathecae absent or 1 pair. ....
- ..... *Microscolex* (part. — *M. dubius* and *M. phosphoreus*)
- 7(6a) a. Spermathecal pores 1 pair, in 7/8. Prostates tubular, extending through several segments, prostate ducts and vasa deferentia of each side fused and both conspicuously thickened, seminal grooves absent ..... *Kayarmacia*
- b. Spermathecae 1 pair, in 8/9. or exceptionally 7/8. Prostates not usually extending through several segments; this ducts and vasa deferentia not thickened or if (*D. retractata*) vasa somewhat thickened, seminal grooves present in posterior half of XVII ..... *Diploptrema* (part.)

***Diplootrema* Spencer, 1900**

*Diplootrema* Spencer, 1900: 31.

**Type species:** *Diplootrema fragilis* Spencer, 1900 (Gayndah, Queensland).

*Eodrilus* Michaelsen, 1907: 141. (Australian species only).

*Diplootrema*; (part. excluding *Notiodrilus* and *Microscolex*) Jamieson 1971b: 100–102.

*Microscolex* (*Diplootrema*); Jamieson and Dyne 1976: 447–448.

*Diplootrema*; Dyne 1987: 1.

**Diagnosis**

Setae 8 per segment. Prostates 2 pairs, tubular, rarely tubuloracemose to racemose, their pores on XVII and XIX; rarely a single pair, on XVII. Male pores a single pair, on XVIII, occasionally in 17/18, or rarely, combined with the prostatic pores on XVII; exceptionally, with prostatic pores in XVII, and male pores at 17/18; spermathecal pores 2 pairs, at 7/8 and 8/9, ventrolateral, or a single pair, at 8/9; rarely transposed to 8/9 and 9/10. Nephropores in a single series on each side, or, exceptionally, alternating regularly between *cd* and a point far dorsal of *d*. Gizzard usually well developed, muscular, in V (or, rarely, in VI?). Calciferous glands present or absent. Holonephric, avascular. Holandric or rarely, metandric. Testis-sacs absent. Penial setae invariably present; genital setae usually present. Nephridial bladders absent.

**Description**

Very small to moderately large amphibious or terrestrial worms (27–230 mm in length) with 100–400 segments. Body circular in cross-section. Prostomium (Fig. 5) pro-epilobous to epilobous. Dorsal and ventral median groove absent. Dorsal pores absent, or commencing from 7/8 to behind the clitellum. Setae very closely paired, though in *D. minuta* *c* and *d* are widely spaced in the hindbody; in 8 longitudinal rows throughout; ventral intersetal distance (*aa*) usually slightly smaller than, never greatly different from that separating the lateral setae (*bc*); ventral and dorsal setal couples (*ab* and *cd*) approximately of equal width (excepting *D. minuta*, posteriorly); dorsal median intersetal distance (*dd*) 40–66% of the body circumference in the forebody (XII). Setae of XVIII unmodified, or the ventral setal couples lacking; ventral couples of XVII and XIX modified as enlarged penial setae, or those of XVII only modified in microscolecine forms; ventral couples of some of segments VII–X (and, exceptionally, XI–XVI?) modified as sculptured and enlarged

genital or copulatory setae (also termed spermathecal setae), or, occasionally, unmodified. Nephropores externally inconspicuous in *c*, shortly below *c* anteriorly, to *cd* posteriorly, or commonly in or above *d* to near the dorsal midline; all nephropores anterior in their segments; rarely (*D. cornutheca*, *D. heteropora*, *D. magnetis*) alternating regularly between *cd* or below and a point far dorsal of *d*. Clitellum annular or saddle-shaped, or a combination of these, occupying XII or, more commonly, XIII to XVI–XX. Two pairs of prostatic pores equatorial on XVII and XIX, from median of *a* to shortly lateral of *b*, or, rarely a single pair of combined male and prostatic pores on XVII; exceptionally, a single pair of prostatic pores, in XVII with male pores in 17/18; a pair of male pores in seminal grooves (the latter sometimes absent?) which link the prostatic pores of a side; male pores usually equatorial, or slightly presetal, and occasionally far anterior in XVIII, near or at 17/18. Accessory genital markings present in some of the segments VIII–XX, usually intersegmental or rarely, absent. Female pores paired, presetal, median to lateral of *ab*, in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, from slightly median of *a* to immediately below *c* lines; rarely in 8/9 only; rarely transposed to 8/9 and 9/10.

Some pre-clitellar septa thickened. Dorsal blood vessel single, or, less commonly, bifurcate intrasegmentally in anterior segments or more extensively; continuous onto the pharynx; last hearts in XIII, exceptionally XII, those in X posteriorly latero-oesophageal, each with connectives from both the dorsal and supra-oesophageal vessels; dorsoventral commissural vessels commencing in VI–VIII; supra-oesophageal vessel limited to the oesophagus; subneural vessel absent. Gizzard large, often strongly muscular, single in V (or, exceptionally, VI?). Calciferous glands absent, or, less commonly, weakly developed as oesophageal pouches; rarely several pairs of well-developed nacreous glands. Intestine commencing in XIV–XVIII (or XIX?); a low to moderately prominent typhlosole usually present, rarely absent. Nephridia avascular exonephric holonephridia, with presetal nephrostomes; tufted nephridia with simple ducts sometimes present in anterior segments (those in IV and V commonly entering the buccal cavity); exceptionally (*D. minuta*) with simple replication to give 2 pairs of nephridia in some segments but not meronephric throughout. Holandric: sperm funnels free in X and XI; metandric: funnels in XI only; or with funnels in X rudimentary. Seminal vesicles 2 pairs, in IX and XII, or XI and XII, or a

single pair in XII only. Prostate glands tortuous tubes either restricted to their segment of origin, or extending posteriad (rarely anteriad) through 1 to many segments, or rarely compact, tubuloracemose to racemose; posterior pairs often conspicuously smaller than the anterior pair; external ducts muscularised but lacking terminal bursae. Penial seta follicles usually with copulatory musculature. Ovaries with multiple chains of oocytes, together with oviducal funnels, in XIII; ovisacs present, or, more usually, absent. Spermathecae uniform in size, or the posterior pair the larger; the single diverticulum, or, two diverticula (a) sessile, clavate, tubular, or linguiform, usually with intramural sperm chambers.

### Distribution

*Australia*: coastal and adjacent inland Queensland, ranging from the vicinity of Narrabri in New South Wales to northern Queensland and across northern Australia to the Kimberley region of Western Australia; with a single species in south-western Australia. The precise northerly limit of the genus in Cape York Peninsula is unknown, the most northerly record being from the vicinity of Weipa. It is thus uncertain whether *Diploptrema* is replaced by the meronephric *Neodiploptrema* further northwards. However, the two genera are sympatric in the Cape Melville National Park and McIlwraith Range (Jamieson 1997; Dyne 1997).

*Extralimital*: Two Mexican acanthodrilids with a single gizzard but otherwise referable to *Diplocardia* were reasonably placed by James (1990) in *Diploptrema* on morphological grounds but their close relationship to Australian species is questionable. Fragoso and Rojas (1994) have erected *Kaxdrilus* for *Diploptrema*-like species of Mexico and Central America with calciferous glands in the region of VII–XII but it is perhaps questionable that the 'pebbly internal texture' in this region in the two species of James (1990) qualifies to be considered calciferous.

### Remarks

Dyne (1987) restored *Diploptrema* to the rank of genus, independent of *Microscolex* and *Notiodrilus* (see also discussion under *Microscolex*).

Jamieson (1971b) first reported that Spencer's (1900) type-description for *Diploptrema fragilis*, and therefore for the genus *Diploptrema*, was incorrect in recognising only a single pair of prostate glands, supposedly opening separately from a pair of male pores on segment XVIII. The re-examined type material of *Diploptrema fragilis* was shown to have the acanthodrilin arrangement of genital pores, with male pores on XVIII and 2 pairs of prostatic pores, in XVII and XIX, an observation confirmed by Dyne and

Jamieson (1998). As stated in the latter paper, there can be no doubt that the examined specimen is conspecific with the material described by Spencer (1900) as *Diploptrema fragilis*, the type of its genus, although this was questioned by Reynolds and Righi (1994). Points of agreement in Spencer's account which confirm the identity of the re-examined specimens are the large oval midventral glandular patch in XVI–XIX, the swollen, glandular appearance of segment VIII and, less important, the epilobous prostomium and two pairs of spermathecae, with pores in 7/8 and 8/9. With respect to the position of the male and prostatic pores, however, Spencer's account is erroneous, a departure from his usual accuracy, possibly because of the small size of the species.

The presence of an additional pair of prostate glands was first indicated, though not acknowledged, by Sweet (1900) in her re-examination of the types of *D. fragilis*. Sweet's fig. 6 shows the posterior end of the supposed single pair of prostates turning forward and narrowing in a way that is consistent with these posterior ends in fact being a second pair of prostates. It is noteworthy that Stephenson (1930) acknowledged the presence of 'accessory prostates' though adhering to the diploptremate interpretation. The central glandular mass observed by Sweet was clearly the large glandular mass termed 'ventral glands' by Dyne and Jamieson (1998).

Reynolds and Righi (1994), who did not examine material and produced no additional evidence, adhered to Spencer's diploptremate interpretation of the male and prostatic pores — a single pair of prostates separate from the male pores on XVIII. It is unparsimonious to suggest, as Reynolds and Righi (1994) have, that the re-examined specimen represents a second species occurring sympatrically at Gayndah which had the distinctive attributes described by Spencer (1900) and noted above for *D. fragilis*, but the different, acanthodrilin, arrangement of prostates unequivocally demonstrated by Jamieson (1971b) and Dyne and Jamieson (1998). We have re-examined the syntypes and there is no admixture of species.

Accepting Spencer's original description, Michaelsen (1910) placed *D. fragilis* within a monotypic section of the Acanthodrilinae, the Diploptremacea. A subsequent examination of New Caledonian species (Michaelsen 1913) genuinely having the male and prostatic ducts separate on XVIII (as erroneously described by Spencer 1900, for *Diploptrema fragilis*), convinced Michaelsen that such an arrangement was closer to the

plutelloid (and hence, megascolecin) grade of organisation than to the acanthodrilin system. Accordingly, the latter species and *D. fragilis* were referred to a separate subgenus within *Plutellus*.

The seemingly transitional condition of the male terminalia in this group resulted in the incorporation of *Plutellus* (*Diploptrema*) into a phylogenetic scheme (Michaelsen 1916, 1921), endorsed and expanded by Stephenson (1930) where it occupied an intermediate position, separating '*Acanthodrilus*' from the truly megascolecin *Plutellus*. The diploptreman condition *sensu* Spencer (1900) of male terminalia was nevertheless confirmed for New Caledonian species which had been referred to '*Plutellus* (*Diploptrema*)' in the Megascolecinae by Michaelsen (1913) and by Jamieson and Bennett (1979) who renamed this entity *Eudiploptrema*. This genus, in the Megascolecinae, is not further relevant to consideration of the internal phylogeny of the Acanthodrilinae.

Demonstration that the type-species of *Diploptrema* Spencer, 1900, has acanthodrilin male pores (Jamieson 1971b) necessitated placing the type-species of *Eodrilus*, *E. cornigravei* Michaelsen, 1907, and some other Australian species of *Eodrilus*, in *Diploptrema* (Jamieson and Dyne 1976). The congeneric position of the two type-species was emphasised by mutual possession of modified, genital setae, with similar ornamentation, in the vicinity of the spermathecal pores. Pickford (1937) had reconstituted *Eodrilus* for acanthodrilin worms lacking nephridial vesicles, present, however, in *Microscolex* and *Acanthodrilus*. In *Acanthodrilus* they were widened J-shaped tubes, and in *Microscolex* they were ovoid or pear-shaped.

The residue of *Eodrilus*, lacking genital setae and not therefore assignable to *Diploptrema*, and lacking the J-shaped vesicles of *Acanthodrilus*, was placed by Jamieson (1971b) in *Notiodrilus*. Re-examination (Jamieson 1974b) of the type-species of *Notiodrilus*, *Acanthodrilus georgianus* Michaelsen, 1888, was considered to indicate that, notwithstanding the variation from acanthodrilin to microscolecin terminalia noted by Michaelsen (1905) and Pickford (1932) in this and other acanthodrilin species, this species differed sufficiently from the type-species of *Microscolex* to justify retention of *Notiodrilus*, though only as a subgenus of *Microscolex*. *Diploptrema* (erroneously given priority over *Microscolex* and *Notiodrilus*) was included in *Microscolex* as a third subgenus.

(It will be seen under the genus *Microscolex*, below, that retention of *Notiodrilus* as a separate entity is, however, questionable). The subgenus *Microscolex* included only three (microscolecin) species, all with nephridial bladders; *Notiodrilus* was a large, heterogeneous group, containing vesiculate and avesiculate species, while the sole unique feature of five species assigned to the avesiculate subgenus *Diploptrema* was the invariable presence of spermathecal genital setae. However, Jamieson and Dyne (1976) added new species to *Diploptrema* which became polythetic in containing forms with or without spermathecal genital setae.

The decision to broaden *Diploptrema* to include species lacking spermathecal genital setae was taken because of the close morphological resemblance of *D. armatissima*, *D. intermedia* and *D. minuta*, all of Dyne and Jamieson, 1976, all lacking spermathecal genital setae, to the majority of *Diploptrema* species described in that paper, which have these setae. It also involved inclusion of *Diploptrema eremia* (Spencer, 1900) (formerly *Acanthodrilus*), for which genital setae were demonstrated for the first time, *D. australis*, which was shown to lack them, and *D. macleayi*, in which the condition of the setae is undescribed. All known holonephric Australian worms with acanthodrilin male terminalia were thus assigned to *Diploptrema* with the exception of *Microscolex macquariensis* (Beddard, 1896) from the subantarctic Macquarie Island.

In the present study, 29 previously unpublished new species and one new subspecies have been added to *Diploptrema*, and, together with the previously known taxa, closely compared to those members of *Microscolex*/*Notiodrilus* available for re-examination or adequately characterised in the literature. This has confirmed that if the more conservative 'ancestral' acanthodrilin characters, including arrangement of male terminalia, number of spermathecae (2 pairs), structure of prostates (tubular), and presence of penial setae, are considered plesiomorphic, and eliminated, the synapomorphic resemblance between the two groups is much diminished.

Table 1 gives some of the more significant differences between *Diploptrema* and *Microscolex* with respect to certain character states. These have been designated as apomorphic (A)/derived or plesiomorphic (P)/presumed ancestral, using the criteria listed by Jamieson (1978).

**Table 1: Comparison of characters in *Diploptrema* and *Microscolex sensu lato*.**

Character	<i>Diploptrema</i>	<i>Microscolex sensu lato</i>
1. Setal couples	Closely paired (P)	Typically, widely spaced (A)
2. Intersetal distance <i>dd</i>	Never <40% u (P)	Usually <35% u (A)
3. Gizzard	Large and muscular (P)	Usually rudimentary (A)
4. Nephridial vesicles	Absent (P)	Usually present (A)
5. Anterior genital setae	Frequently present (P)	Absent (A)
6. Position of last hearts	XIII (1 exception) (A)	XII (P)
7. Spermathecal diverticula	1, exceptionally 2; usually sessile (P?)	2, exceptionally 1; usually clavate, well demarcated (A?)

When the geographical discontinuity of the two groups is also taken into account, there remains little to justify retention of *Diploptrema* within *Microscolex*. It should be remembered that in the case of individual species deviant from either group for a particular characteristic (e.g. some *Diploptrema* species lack spermathecal genital setae), there is other overwhelming morphological evidence to place them within those respective groups. As noted above, presence of spermathecal genital setae, once considered to be diagnostic of *Diploptrema*, must now be regarded as a synapomorphy of its clade (including some other genera) and therefore plesiomorphic for its members.

The peculiarly scalloped ornamentation of the genital setae in at least *Acanthodrilus*, *Diploptrema* and *Diplocardia*, militates against regarding their genital setae as convergently acquired. Whether

genital setae in the *Balanteodrilus*, and ?some 'Eodrilus' (Central America), some meronephric taxa, e.g. *Lenogaster* (Oriental Region), represent common origin or parallelism remains debatable. The constant absence of genital setae in *Microscolex sensu lato* and other Acanthodriline genera is presumed to represent a secondary loss, as noted above.

Of the relevant characters of *Diploptrema* and *Microscolex sensu lato* employed in Table 1, *Diploptrema* has by far the greater number of plesiomorphic states. *Microscolex* is therefore apomorphic for this character set relative to *Diploptrema*, even though the clade containing *Diploptrema* contains unusual divergent groups, characterised by major apomorphies, within Australia (including the microscolecin *Kayarmacia*, the meronephric *Neodiploptrema* and the balantin *Torresiella*).

## (A) QUEENSLAND SPECIES

### *Diploptrema* (Acanthodrilin Queensland species)

1. *Diploptrema acropetra* Jamieson, 1997
2. *Diploptrema armifera* sp. nov.
3. *Diploptrema athertoni* sp. nov.
4. *Diploptrema attenuata* Jamieson, 1997
5. *Diploptrema australis* (Michaelsen, 1889) (*Acanthodrilus*)
6. *Diploptrema bidiverticulata* sp. nov.
7. *Diploptrema bifistularis* sp. nov.
8. *Diploptrema biloela* Blakemore, 1997
9. *Diploptrema boardmani* sp. nov.
10. *Diploptrema bulburinensis* sp. nov.
11. *Diploptrema capella* Blakemore, 1997
12. *Diploptrema capricorniae* sp. nov.
13. *Diploptrema tyagarah carnarvoni* subsp. nov.
14. *Diploptrema conwayi* sp. nov.
15. *Diploptrema cornutheca* sp. nov.
16. *Diploptrema crateris* sp. nov.
17. *Diploptrema daemeli* (Michaelsen, 1910) (*Eodrilus*)
18. *Diploptrema elstobi* Blakemore, 1997
19. *Diploptrema eungellae* sp. nov.
20. *Diploptrema falcatooides* sp. nov.
21. *Diploptrema fragilis* Spencer, 1900
22. *Diploptrema glareaphila* sp. nov.
23. *Diploptrema helonoma* Dyne and Jamieson, 1998
24. *Diploptrema heteropora* Dyne, 1979a
25. *Diploptrema ingrami* sp. nov.
26. *Diploptrema inornata* sp. nov.
27. *Diploptrema lamberti* sp. nov.
28. *Diploptrema longiductis* sp. nov.
29. *Diploptrema magna* sp. nov.
30. *Diploptrema magnetis* sp. nov.
31. *Diploptrema montislewisi* sp. nov.
32. *Diploptrema narayensis* Blakemore, 1997
33. *Diploptrema nemoralis* sp. nov.
34. *Diploptrema peraeintestinalis* sp. nov.
35. *Diploptrema proserpinensis* Dyne and Jamieson, 1995
36. *Diploptrema pseudospectabilis* sp. nov.
37. *Diploptrema quasifragilis* sp. nov.
38. *Diploptrema queenslandicus* (Michaelsen, 1910) (*Eodrilus*)
39. *Diploptrema rigida* sp. nov.
40. *Diploptrema scheltingai* Jamieson, 1997
41. *Diploptrema schmardae* (Beddard, 1892) (*Acanthodrilus*). Species dubium?
42. *Diploptrema spectabilis* sp. nov.
43. *Diploptrema spenceri* sp. nov.
44. *Diploptrema sulcata* sp. nov.
45. *Diploptrema tenuiseta* sp. nov.

### *Diploptrema* (Microscolecina Queensland species)

46. *Diploptrema glandifera* (Jamieson, 1995) (*Rhododrilus*). New combination
47. *Diploptrema pseudospectabilis* sp. nov.
48. *Diploptrema retractata* sp. nov.

## (B) NEW SOUTH WALES

### *Diploptrema* (Acanthodrilin New South Wales species)

49. *Diploptrema tyagarah* Dyne, 1979b

## (C) WESTERN AUSTRALIA

### *Diploptrema* (Acanthodrilin Western Australian species)

50. *Diploptrema macleayi* (Fletcher, 1890) (*Acanthodrilus*)
51. *Diploptrema cornigravei* (Michaelsen, 1907) (*Eodrilus*)

**(D) NORTHERN TERRITORY*****Diploptrema* (Acanthodrilin Northern Territory species)**

- |  |  |
|--|--|
| 52. <i>Diploptrema armatissima</i> Jamieson and Dyne, 1976             | 57. <i>Diploptrema melaleuca</i> Jamieson and Dyne, 1976 |
| 53. <i>Diploptrema eremia</i> (Spencer, 1896) ( <i>Acanthodrilus</i> ) | 58. <i>Diploptrema minuta</i> Jamieson and Dyne, 1976    |
| 54. <i>Diploptrema insularis</i> Jamieson and Dyne, 1976               | 59. <i>Diploptrema planumfluvialis</i> Dyne, 1987        |
| 55. <i>Diploptrema intermedia</i> Jamieson and Dyne, 1976              | 60. <i>Diploptrema ridei</i> Jamieson and Dyne, 1976     |
| 56. <i>Diploptrema mantoni</i> Jamieson and Dyne, 1976                 | 61. <i>Diploptrema shandi</i> Jamieson and Dyne, 1976    |
|  | 62. <i>Diploptrema socialis</i> Dyne, 1987               |

***Diploptrema* (Microscolecina Northern Territory species)**

63. *Diploptrema gracilis* sp. nov.

**KEY TO THE *DIPLOPTREMA* SPECIES OF QUEENSLAND AND NEW SOUTH WALES**

*D. schmardae*, from Queensland, is omitted from the key as insufficiently described.

A single known species, *Diploptrema tyagarah*, in NSW, with a subspecies in Queensland.

- 1 a. Two pairs of prostatic pores, on XVII and XIX, male pores separate, on XVIII, or at 17/18 (*Acanthodrilin* species) . . . . . 4
- b. A single pair of prostatic pores either combined with the male pores in XVII, or the male pores separate, in 17/18 (*Microscolecina* species) . . . . . 2
- 2(1b) a. Genital markings including a pair of distinct papillae in intersegmental furrow 11/12, in *bc*. Genital setae absent. No visible seminal grooves . . . . . 3
- b. Genital markings not including a pair of distinct papillae in intersegmental furrow 11/12. Genital setae present in IX. A pair of deep, sharply defined seminal grooves running from the combined male and prostatic pores to anterior edge of XVIII . . . . . *D. retractata*
- 3(2a) a. Genital markings restricted to a pair of distinct papillae in intersegmental furrow 11/12, in *bc*. –XV. (Small worms, 58 mm) . . . . . *D. glandifera*
- b. Genital markings including a pair of distinct papillae in intersegmental furrow 11/12, in *bc* but also in 12/13 and with transverse midventral pads in several clitellar and postclitellar segments. (Large worms, 200 mm) . . . . . *D. pseudospectabilis*
- 4(1a) a. Enlarged, modified genital setae present in at least one segment anterior to the female pores . . . . . 5
- b. Enlarged and/or modified genital setae absent . . . . . 30
- 5(4a) a. Spermathecal pores in 7/8 and 8/9 in or near *ab*. . . . . 6
- b. Spermathecal pores in 7/8 and 8/9 shortly median of *c* lines . . . . . *D. daemeli*
- c. Spermathecal pores in 8/9 and 9/10 . . . . . *D. acropetra*

- 6(5a) a. Male pores slightly, or well lateral of *a* or *b* lines ..... 7  
 b. Male pores median of *a*–IX ..... ***D. queenslandica***
- 7(6a) a. Nephropores alternating regularly between mid *bc* or *cd*, and a point well above *d* ..... 8  
 b. Nephropores (at least on the clitellum) in a single, non-alternating but sometimes irregular series, usually in *cd*, sometimes above *d*, exceptionally in *b* lines ..... 10
- 8(7a) a. Prostate glands tubular, highly coiled ..... 9  
 b. Prostate glands compact, tubulo-racemose ..... ***D. ingrami***
- 9(8a) a. Genital seta follicles a single pair, in VIII; spermathecal diverticulum bipartite, forming conspicuous, 2 cornute outpouchings; duct short .....  
 ..... ***D. cornutheca***  
 b. Genital seta follicles 2 pairs, in VIII and IX; spermathecal diverticulum single, sessile; duct long ..... ***D. heteropora***
- 10(7b) a. Male gonads holandric ..... 13  
 b. Male gonads metandric or incipiently so ..... 11
- 11(10b) a. Vestigial funnels present in X, nephropores well dorsal of *d* lines .....  
 ..... ***D. crateris***  
 b. Spermatic funnels completely lacking in X; nephropores in *d* lines or in *cd* ..... 12
- 12(11b) a. Genital markings include large, unpaired, tumid pads in some of the following: 15/16, 16/17, 20/21–23/24; genital setae rudimentary, in X–XII .....  
 ..... ***D. bulburinensis***  
 b. Tumid pads lacking, genital setae well developed, in XII and XIII .....  
 ..... ***D. lamberti***
- 13(10a) a. Tufted nephridia in and/or anterior to IV ..... 14  
 b. Tufted nephridia absent ..... 15
- 14(13a) a. Dorsal blood vessel intrasegmentally bifurcate in the oesophageal region; 3 pairs of genital seta follicles present in VII–X ..... ***D. bifistularis***  
 b. Dorsal blood vessel single throughout; 3 pairs of genital seta follicles present in X–XII ..... ***D. boardmani***
- 15(13b)a. Nephropores located well above *d* lines ..... 16  
 b. Nephropores in the vicinity of *b* or *cd* lines ..... 19
- 16(15a) a. Male pores at the extreme anterior margin of XVIII, near or at 17/18 .....  
 ..... 17  
 b. Male pores equatorial, in XVIII. (Penial setae very large, ectally clothed with short, narrow spines) ..... ***D. eungellae***
- 17(16a) a. Ventral setal pairs present on XVIII ..... ***D. conwayi***  
 b. Ventral setal pairs absent from XVIII ..... 18



- 18(17b) a. Spermathecal diverticulum distinct from, and approximately equal in volume to, the ampulla; duct short . . . . . *D. armifera*  
 b. Spermathecal diverticulum considerably smaller than, and sessile on, the ampulla; duct long and sinuous . . . . . *D. longiductis*
- 19(15b) a. Male pores at the extreme anterior margin of XVIII, near or at 17/18 . . . . 41  
 b. Male pores equatorial, or slightly anterior to the setal arc, in XVIII . . . . 20
- 20(19b) a. Dorsal pores present . . . . . 22  
 b. Dorsal pores absent . . . . . 21
- 21(20b) a. Genital markings include a midventral pad, bearing paired papillae, in some of 10/11–14/15 a diagnostic pair of papillae on XVIII, and a transverse pad often on XX . . . . . *D. attenuata*  
 b. Genital markings only a single midventral pad on XX . . . . *D. proserpinensis*
- 22(20a) a. Ectal end of penial setae inrolled; a single pair of seminal vesicles in XII. Large, unpaired median genital markings invariably present in 10/11 and 21/22; may have midventral markings in 14/15, 15/16; also paired genital seta tumescences in VIII . . . . . *D. rigida*  
 b. Not as 'a' (Difference in penial setae assumed for Blakemore species, for which ornamentation not described). . . . . 23
- 23(22b) a. Depressed glandular patches extending over XVI–XIX; genital markings include midventral pads in 18/19 and 19/20. . . . . 24  
 b. Genital field not as 'a', though sometimes including 18/19 and 19/20 . . . . . 25
- 24(23a) a. Ventral setal pairs of XVIII absent; seminal vesicles in IX and XII. Ventral genital markings present in 16/17. Anterior and posterior prostates approximately equal in size . . . . . *D. narayensis*  
 b. Ventral setal pairs of XVIII present; seminal vesicles in XI and XII. Ventral genital markings absent from 16/17. Anterior prostates considerably larger than posterior pair . . . . . *D. fragilis*
- 25(23b) a. Prostates tubuloracemose. A transverse bar joins the male papillae on XVIII . . . . . *D. scheltingai*  
 b. Prostates tubular. Male pores not connected by a transverse bar . . . . . 26
- 26(25b) a. Dorsal blood vessel double. Genital markings absent but genital setae on paired raised tumescences on (VII), VIII and IX . . . . . *D. biloela*  
 b. Dorsal blood vessel single. Genital markings present . . . . . 27
- 27(26b) a. Genital markings a large, unpaired, median tumescence in 16/17, and 19/20. Conspicuous genital seta follicles in VIII and IX, associated with the spermathecae; accompanied by prostate-like glands, with definite central lumen, and small ducts . . . . . *D. helonoma*  
 b. Genital markings and genital seta follicles not as 'a' . . . . . 28

- 28(27b) a. Dorsal pores, from 11/12 or 12/13 ..... 42  
 b. Male field not as 'a'. Dorsal pore 7/8 or 8/9 ..... 29
- 29(28b) a. Genital markings include a midventral slightly glandular area with pore-like centre, in 17/18 and 18/19; a large transversely elliptical tumescence in XVI; a diffusely glandular area immediately posterior to the male field, extending to 20/21, and within it, a faintly visible marking, similar to those within the male field, median, in XIX, close to 19/20 (*D. tyagarah tyagarah*) or a single median pad, with paired tubercles, in XVI and more closely paired in 19/20 (*D. tyagarah carnarvoni*) ..... ***D. tyagarah***  
 b. Genital markings small paired ventral markings in XVI, wider and just median to male pores on XVIII, and in 18/19 and 19/20 ..... ***D. capella***
- 30(4b) a. Male gonads holandric ..... 32  
 b. Male gonads metandric ..... 31
- 31(30b) a. Nephropores alternating regularly between a point below *c* lines and one well above *d* lines ..... ***D. magnetis***  
 b. Nephropores in a single series, above *d* lines ..... ***D. magna***
- 32(30a) a. A pair of calciferous glands arising in XV and extending to XVII ..... ***D. spenceri***  
 b. Calciferous glands not so arranged or, usually, absent ..... 33
- 33(32b) a. Seminal vesicles present in IX and XII ..... 34  
 b. Seminal vesicles present in XI and XII ..... 38  
 c. Seminal vesicles present in IX, XI and XII. Nephropores far dorsal of *d* lines ..... ***D. australis***
- 34(33a) a. Ventral setal pairs absent from XVIII ..... ***D. inornata***  
 b. Ventral setal pairs present on XVIII ..... 35
- 35(34b) a. Male pores postsetal, in XVIII; a single, large, tumid pad present in 12/13 .. ***D. capricorniae***  
 b. Male pores equatorial or presetal, in XVIII; genital markings not as above . . . . . 36
- 36(35b) a. Large worms (200 mm). Male pores almost at 17/18. A prominent pair of tubercular swellings in 11/12. Dorsal blood vessel bifid ..... ***D. spectabilis***  
 b. Morphology not as above. .... 37
- 37(36b) a. Oesophagous with 4 to 6 pairs of calciferous glands or diverticula in X, XII–XV. Each spermatheca with a single diverticulum ..... 43  
 b. Oesophagus lacking diverticula. Each spermatheca with two diverticula . . . . . ***D. bidiverticulata***

- 38(33b) a. Male field containing a deep, rectangular concavity. Genital markings include a pair of eye-like markings in each of 11/12 and 12/13; usually with a series of transverse depressions in some or all of 20/21–22/23. Penial setae broad, flattened, unornamented–22/23. Penial setae broad, flattened, unornamented 28  
 ..... ***D. falcatoides***  
 b. Morphology not as above ..... 39
- 39(38b) a. Seminal grooves forming distinct clefts; ectal ends of the penial setae attenuating abruptly ..... ***D. sulcata***  
 b. Seminal grooves superficial; ectal ends of the penial setae tapering gradually  
 ..... 40
- 40(39b) a. Penial setae stout; a long series of genital markings present in 10/11–15/16 and 20/21–23/24 ..... ***D. nemoralis***  
 b. Penial setae long, thin, and clothed with fine spines ectally; genital markings restricted to 10/11 and 21/22–23/24. .... ***D. tenuiseta***
- 41(19a) a. Genital markings typically include a small intersegmental pad in 13/14; a small, rounded marking equatorial in 14/15; and 3 rather faint intersegmental markings in 19/20–21/22. Oesophagus produced into digitiform projections in X–XIV; penial setae with spatulate tip. Dorsal blood vessel single .....  
 ..... ***D. athertoni***  
 b. Genital markings typically include a series of regular, raised, intersegmental strips extending across bb (or slightly beyond), in some of 15/16, 16/17, 19/20–24/25. Oesophagus in XII–XIV dilated, highly vascularised and internal rugose but diverticula absent. Penial setae not spatulate. Dorsal blood vessel bifid . . .  
 ..... ***D. glareaphila***
- 42(28a) a. Four genital markings in the male field, in 16/17–19/20. Setae retained on XVIII ..... ***D. elstobi***  
 b. Genital markings include a distorted ellipsoidal marking, median, in 16/17; single or paired small, rounded, blister-like markings medially in the central concavities centred on 17/18 and 18/19. Ventral setal couples absent on XVIII  
 ..... ***D. quasifragilis***
- 43(37a) a. Reniform calciferous glands or diverticula arising ventrolaterally on thin stalks, paired in each of XII–XV. Spermathecal pores intrasegmental, in VIII and IX ..... ***D. montislewisi***  
 b. Vento-lateral diverticula in X–XV (those in X and XI short and virtually sessile; those in XII–XV well demarcated sacciform projections with internal lamellae. Spermathecal pores intersegmental, in 7/8 and 8/9 .....  
 ..... ***D. peraeintestinalis***

**KEY TO THE *DIPLOPTREMA* SPECIES OF THE NORTHERN TERRITORY**

- 1a a. Prostatic pores two pairs, in XVII and XIX ..... 2  
 b. Prostatic pores one pair, in XVII ..... *D. gracilis*
- 2(1a) a. Dorsal pores commencing behind the clitellum. Seminal vesicles in IX and XII ..... *D. eremia*  
 b. Dorsal pores commencing in 7/8 to. 11/12 or (*socialis*) absent? Seminal vesicles in XI and XII, or in XII only, exceptionally in IX and XII ..... 3
- 3(2b) a. Spermathecal diverticulum longer, rarely slightly shorter, than the ampulla plus duct, tubular or tongue-shaped ..... 4  
 b. Spermathecal diverticulum as long as or, usually, much shorter than the ampulla plus duct, clavate or bulbous ..... 9
- 4(3a) a. Spermathecal diverticulum an elongate, blind, ectally widening tube; through most or all of its length much narrower than the ampulla. Seminal chambers in diverticulum walls very numerous and very small ..... 5  
 b. Spermathecal diverticulum broad, depressed, tongue-like, as wide as or wider than the ampulla. Seminal chambers in diverticulum walls moderately numerous but large and giving the diverticulum a slightly lobulated appearance VI forming large tufts with many spiral loops. Nephropores throughout far lateral of *d* lines. Seminal vesicles in XI and XII ..... 6
- 5(4a). a. Nephridia in some of segments II-VII forming large tufts with many spiral loops. Nephropores throughout far lateral of *d* lines. Seminal vesicles in XI and XII ..... 6  
 b. Nephridia not tufted though anteriorly they may be complexly coiled. Nephropores in *d* lines. Seminal vesicles in XII or XI and XII ..... 7
- 6(5a) a. Transverse ventral intersegmental padlike genital markings with paired 'pores' in at least 13/14, 14/15, and 15/16 ..... *D. insularis*  
 b. Transverse intersegmental genital markings absent from 13/14-15/16 but a transverse groove-like marking or series of markings in 16/17 usually flanked by 2 longitudinally aligned circular markings on each side postsetally in XVI and at 16/17 ..... *D. melaleuca*
- 7(5b) a. Seminal vesicles in XII only. Genital markings include a midventral subrectangular pad, with pore-like areas in *ab*, intersegmental in one or more of 8/9, 10/11 and 12/13; paired (sometimes unilateral) circular intersegmental in one or more of 13/14; 14/15; 16/17; 19/20 or typically conjoined to give a large pad in 21/22 ..... *D. intermedia*  
 b. Seminal vesicles in XI and XII. Genital markings an intersegmental tumescence with pore like centre in *ab* in 14/15; a similar marking on the left in 26/27 ..... *D. armatissima*
- 8(4b) a. Transverse ventral pad-like genital markings with paired or triple 'pores' present in some or all of intersegments 10/11 to 14/15, 16/17 and 19/20 to 21/22 but not in 15/16 ..... *D. ridei ridei*

- b. Transverse ventral pad-like or rounded genital markings, with or without paired pores, present in some or all of 10/11–16/17 and 21/22–24/25 ..... *D. ridei melvillensis*
- 9(3b) a. Last hearts in XII. Intestine commencing in XIV. Genital markings usually absent or a circular marking with a pore-like centre paired in *ab* postsetally in VIII or paired median to a posteriorly in XVI ..... *D. minuta*
- b. Last hearts in XIII. Intestine commencing in XV–XVII. Genital markings not as above ..... 10
- 10(9b) a. Prostates limited to the segment of origin. Genital markings four conspicuous, broad tumid bands almost cover the ventral surface of segments VII–X ..... *D. planumfluvialis*
- b. Prostates extending through more than one segment ..... 11
- 11(10a) a. Nephropores above *d* lines. Genital markings present in most intersegments 10/11–14/15 and 16/17. Seminal vesicles in XII only ..... *D. mantoni*
- b. Nephropores in *d* lines. Seminal vesicles in IX and XII ..... 12
- 12(11b) a. First dorsal pore 7/8. Genital markings present in 16/17 but absent from 10/11–14/15 ..... *D. shandi*
- b. Dorsal pores not apparent. No genital markings known ..... *D. socialis*

### ACANTHODRILIN QUEENSLAND *DIPLOPTREMA* SPECIES

#### *Diploptrema acropetra* Jamieson, 1997

(Figs 6–8)

*Diploptrema acropetra* Jamieson, 1997: 233–237, figs 1–4, 39.

**TYPE LOCALITY:** Qld, 144°46.75'S 14°43.9'E, Rocky Peak, Cape Melville National Park, altitude 450 m, on sandstone plateau, base of trees where pigs had been digging, edge of *Banksia robur* swamp. Coll. K.R. McDonald, P.J. Lethbridge, 4 Apr 1995.

**HOLOTYPE:** QM G212027 (includes microscope slide of right genital seta of IX).

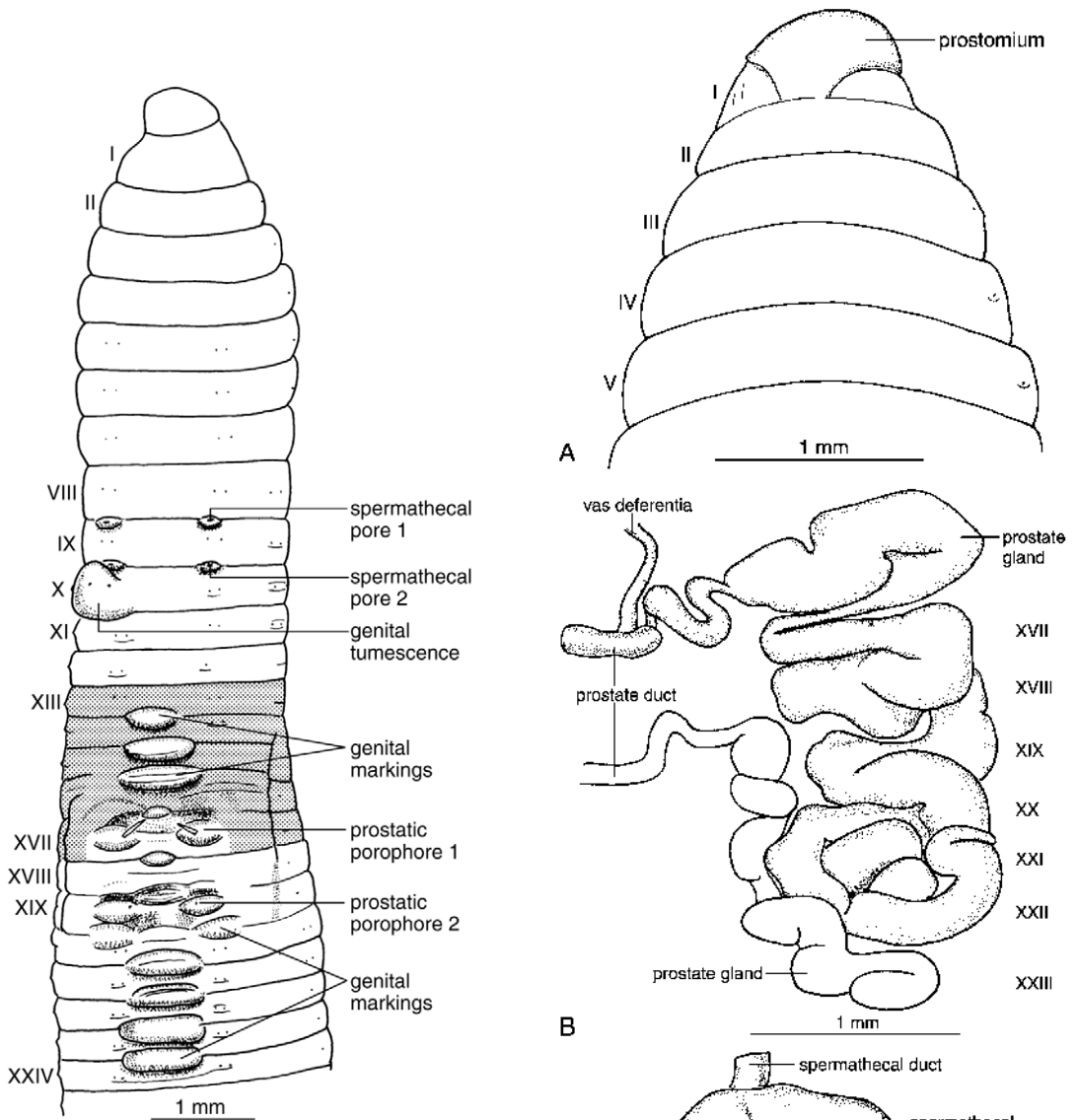
**PARATYPES:** P1–9 QM G212028–212036.

**OTHER MATERIAL:** Several not designated types, QM G213391.

#### Description (after Jamieson 1997)

Length 38–55 mm. Width (midclitellar) 1.7–2.4 mm. Segments 163–169. Pigmentless buff in ethanol. Prostomium large, epilobous 1/2, closed, the lateral margins of the dorsal tongue strongly convergent and concave or prolobous with longitudinal grooves on the peristomium giving an impression of an epilobous condition. Peristomium

longer than segment II; neither it nor the prostomium bisected ventrally. Dorsal pores poorly visible, commencing on or behind the clitellum. Setae 8 per segment, commencing on II; in XII, *aa: ab: bc: cd: dd* = 7.2: 1.0: 6.6: 0.7: 29.2; or 13.6: 1.9: 12.5: 1.3: 55.1%; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; ventral setae of X forming genital setae. Nephropores not visible. Clitellum in XIII–XVII, annular, but interrupted ventrally in XVII by the prostatic porophores. Male pores not visible. Prostatic porophores 2 pairs, in XVII and XIX, each an elliptical papilla centred approximately in *ab* lines; penial setae protuberant from one or both pairs; seminal grooves not apparent or a faint outwardly curved (parenthetic) groove connecting the prostatic pores on each side. Genital tumescences: unilateral or paired in X; paired or absent in XI. Genital markings: an unpaired midventral elliptical to rounded oblong pad between the ventral setal couples (in *aa*) in each of intersegmental furrows 13/14–15/16, 16/17, 17/18, 20/21–23/24; those in 16/17 and 17/18 small; a suggestion of a pad sometimes present in 18/19. Female pores not visible. Spermathecal pores 2 pairs, in 8/9 and 9/10.

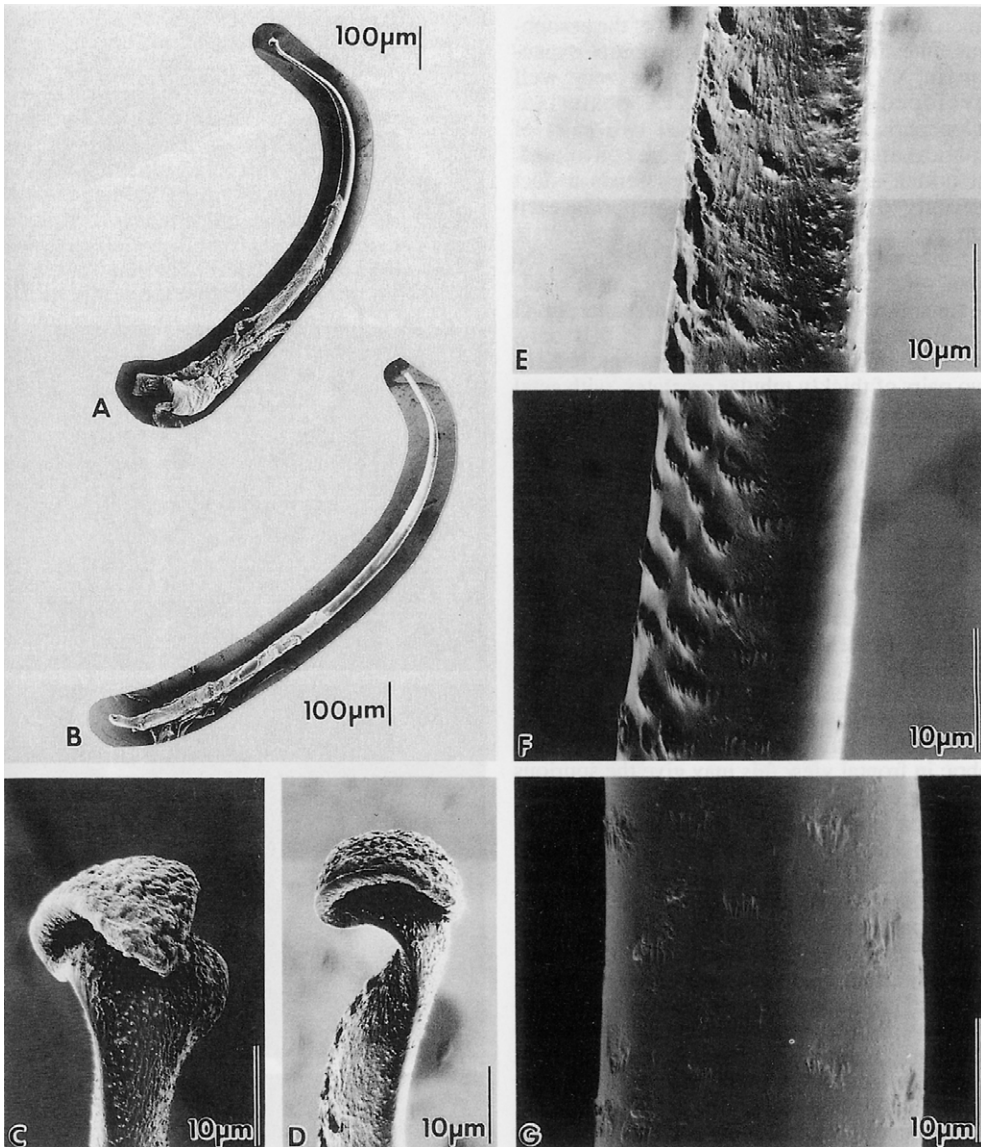


**Fig. 6.** *Diploptrema acropetra* Jamieson, 1997, Holotype (clitellum drawn from paratype 1).  
[After Jamieson 1997]

Septa 8/9 and 9/10 the thickest, fairly strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; in XI–XIII stout, latero-oesophageal, the connectives to the supra-oesophageal vessel being wide, those to the dorsal vessel scarcely apparent; commissurals in X anteriorly slender, with dorsal connectives only. Gizzard very large, an elongate, glossy, muscular

C

**Fig. 7.** *Diploptrema acropetra* Jamieson, 1997, Holotype: A anterior end; B, right prostates; C, right spermatheca of IX.  
[After Jamieson 1997]



**Fig. 8.** *Diploptrema acropetra* Jamieson, 1997, Holotype: **A** and **B**, two right penial setae of XIX; **C** and **D**, different views of the seta shown in **A**; **E-G**, successively more posterior to near the basal region of same. [From Jamieson 1997]

cylinder about three times longer than wide, in V, but its posterior end at the level of segment X. Oesophagus segmentally dilated, and longitudinally compressed, in each of XIV–XVI; the walls in these segments with numerous closely situated, deep, internal lamellae but lumen not constricted off from that of the oesophagus. Intestine commencing with abrupt expansion in XVIII. Dorsal typhlosole very well developed from about XXIX posteriad. Holonephric throughout;

at least two pairs of nephridia anterior to the gizzard are convoluted, not tufted, and each nephridium sends a duct anteriorly to the pharynx. Typical nephridia each with preseptal funnel and slender, avesciculate duct discharging presetally in the vicinity of the dorsal setal couples (*cd*). Metandric; large seminal funnels, with spermatozoal iridescence, in XI only. Seminal vesicles racemose, in XII only. Flattened ovaries, with many egg strings, in XIII. Two pairs of thickly

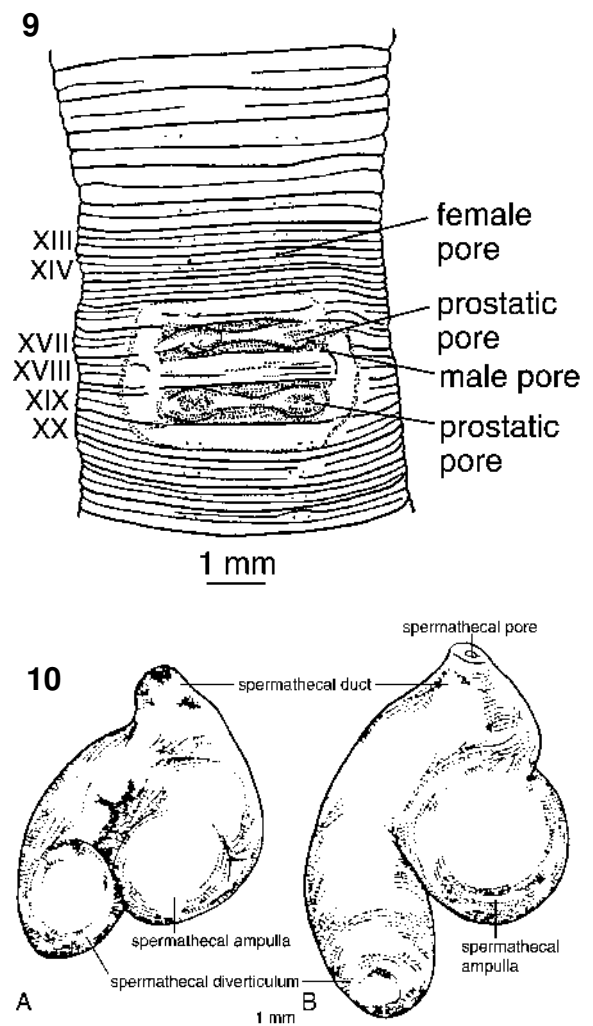
tubular prostates, with ectal ducts discharging in XVII and XIX. The anterior pair is very much the larger and winds from XVII to XXII; the tortuous muscular duct is joined near its ectal end by the thick, vas deferens, the width of which, greatly exceeding that of a normal vas, suggests that it is a sperm reservoir. Posterior prostates winding from XIX to XXIII; the ectal duct shorter, though still long, less tortuous and poorly muscularised. Both pairs of prostate ducts overlain by penisetal follicles. Penial setae curved through a right angle or slightly less; the tip widened recurved 'dorsally' for a short distance before curving 'ventrally' to a V-shaped tip, the tip thus having the appearance of a poised cobra; in frontal view this may give the spurious appearance of a ladle-shape; sculpturing in the midregion consisting of palisades of pointed scales in incomplete circlets, the circlets being spaced longitudinally at approximately 10  $\mu$ m intervals; the scales sparser basally; some groups of scales continuing to, but not including, the modified tip; alternatively the scales may form small obliquely arranged groups, each group consisting of a small protuberant semicircle of pointed teeth which overlie a depression, so that the seta resembles a grater; length of a well-developed right penial seta 1 mm. Genital setae present at the tumescences in X or X and XI; each with the usual diploptreman appearance, a stout seta with four opposed longitudinal series of long notches and the tip slightly expanded below the terminal point; the seta gently curved; the longitudinal notches confined to approximately the ectal third; length right seta of IX (measured in a straight line from tip to base) = 0.9 mm; greatest width, near base, 60  $\mu$ m. Spermathecae two pairs, transposed posteriorly one segment, relative to the usual megascolecoid condition, so that the posterior pair is in X, the anterior pair in IX. The posterior pair of spermathecae, in X, very much larger than the anterior pair; each posterior spermatheca with a sacciform ampulla, a short narrow duct; and a large multiloculate and apically lobed diverticulum, containing sperm bundles, which joins the junction of ampulla and duct and is elongated at approximately a right angle to the duct. Length right spermatheca of X = 1.5 mm; length ampulla = 1.0 mm; ratio length spermatheca: length duct (including base of diverticulum) = 3.5; length of diverticulum lateral of duct = 0.6 mm. The diverticula of the anterior spermathecae are small 'rosettes' of loculi.

### Remarks

As noted by Jamieson (1997), transposition of the spermathecae, from the usual position in VIII and IX to IX and X, is unknown elsewhere in *Diploptrema*. This coexists with the unusual slender condition of the commissural blood vessels, and

suppression of testes and funnels in X, giving the metandric condition. As the prostatic porophores are in their normal segments of XVII and XIX, it is clearly not due to interpolation of a segment, as occurs in some species of the closely related genus *Acanthodrilus*, in New Caledonia (Jamieson and Bennett 1979).

Rocky Peak is an isolated upland plateau of Battle Camp sandstone, adjacent to the Deighton Tableland. The swampy habitat is the most northerly location of a habitat type dominated by *Banksia robur*.



**Figs 9, 10, *Diploptrema armifera* sp. nov.** 9, genital field of Holotype; 10: A, left spermatheca of VIII, Holotype; B, right spermatheca of IX, Paratype 1.



***Diplootrema armifera* sp. nov.**

(Figs 9, 10)

**TYPE LOCALITY:** Qld, 18°47'S 146°09'E, Waterfall Creek, near its intersection with the Bruce Hwy, 25 km south of Ingham, in dark alluvium high up the creek bank. Coll. G. Dyne and D. Lambert, 5 Feb 1974.

**HOLOTYPE:** QM GH2930.

**PARATYPE:** QM GH2946.

**OTHER MATERIAL:** 18°38'S 146°10'E, Herbert River, Ingham, near riverbank. Coll. H.J. Lohman 8 Aug 1970, lodgement unknown.

**Description**

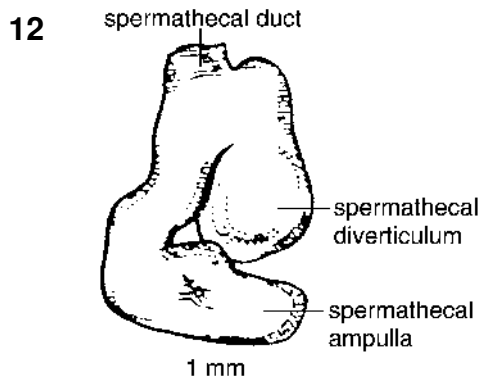
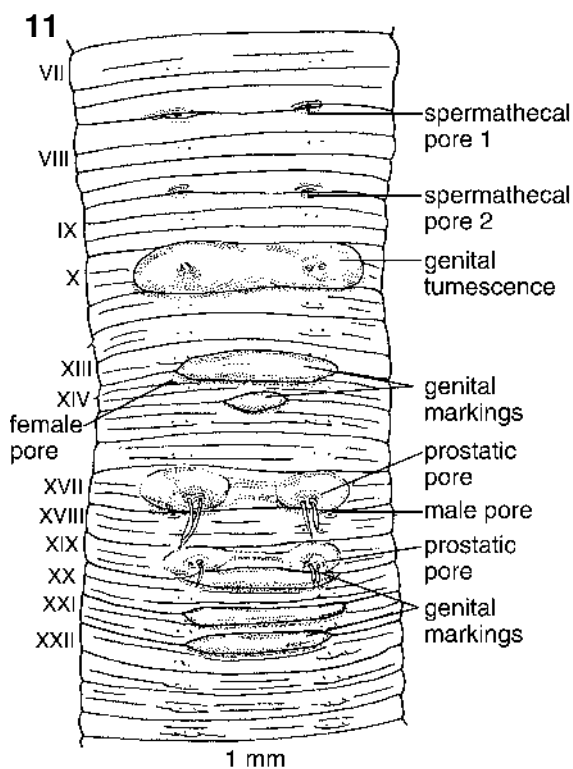
Length 76, 80 mm. Width 5.7, 5.6 mm. Segments 178, 173. (H, P1). Uniformly circular in cross-section, pigmentless grey-buff in alcohol. Prostomium pro-epilobous. First dorsal pore 11/12. Setae 8 per segment; ventral setal couples of XVIII absent; those of XVII and XIX modified as much enlarged penial setae; those of VII modified as genital setae. Nephropores not visible externally. Clitellum not developed, the male field consisting of an oval, glandular area, with raised lateral rims and a depressed inner field. A median raised strip traverses the area within segment XVIII; the male porophores are atop rounded papillae in XVII and XIX, in stark relief within the depression. The prostatic pores of a side are joined by a shallow, arcing seminal groove, which runs laterally, along the rim of the male field, and where it is at its widest. Male pores are barely within XVIII, immediately posterior of the 17/18 intersegment, in *bc*. Genital markings slight glandular swellings associated with the genital setae, in VII (H, P1, P2); no other markings discernible. Female pores on XIV, slightly presetal, in *a* lines (approximately). Spermathecal pores are inconspicuous orifices in 7/8 and 8/9, aligned with setal row *a*.

Septa 5/6 thin, encapsulating the gizzard, 6/7–7/8 moderately thickened 8/9–9/10 well-muscularised, 10/11 weaker, remainder diaphanous. Dorsal blood vessel single; last hearts in XIII; the commissurals of XII and XIII only heart-like and latero-oesophageal, with connectives from both dorsal and supra-oesophageal vessels. Remaining commissurals dorsoventral only, and decreasing in size anteriorly. A long portion of undifferentiated oesophagus separates the pharyngeal mass from the gizzard; the latter is strongly developed, barrel-shaped, and incompressible, in V; the anterior rim firm. Oesophagus narrow, internally rugose, with 3 pairs of essentially dorsal, conspicuous, sac-like

outpouchings in XII–XIV (those in XIII considerably smaller than the other 2 pairs — H); these outgrowths are internally lamellate, and highly vascularised, communicating freely with the oesophagus, though not stalked. Intestine commences in XVIII, a low dorsal typhlosole present behind XXVII. Simple, stomate holonephridia are present throughout, their ducts somewhat irregular in their disposition, entering the parietes some distance (approx. equal to *bc*) above *d* lines. There is some variation in the position of exit of the ducts (and therefore of the nephropores?), though without any apparent pattern; terminal ends of some ducts slightly swollen due to the encystment of small nematodes; tufted nephridia absent from the pharyngeal region. Holandric; 2 pairs of small to medium, faintly iridescent sperm funnels in X and XI, and 2 pairs of small, compactly racemose seminal vesicles in XI and XII. Two pairs of tightly coiled tubular prostates lie in their segments of origin, XVII and XIX; ducts long, tortuous, and with conspicuous muscular sheen. Penisetal follicles intimately associated with the prostatic apparatus, *a* and *b* follicles discrete; each is connected to the body wall by a thick muscular band (= copulatory musculature), the individual ligaments of each pair of follicles fusing just prior to insertion on the body wall. Each of the follicles with numerous long reserve setae; the setae essentially straight though curving sharply over their ectal  $\frac{1}{3}$ ; the distal  $\frac{1}{4}$  has a light scattering of fine spinules, the tip invariably recurved. Length of mature seta 7.12 mm; midshaft diameter 59  $\mu$ m (mean of 4). Ovaries, and small funnels present in XIII, ovisacs not demonstrable. Spermathecae 2 pairs, in VIII and IX; each comprises a digitiform ampulla, a bulbous, inseminated diverticulum broadly fused to the ectal  $\frac{1}{2}$  of the ampulla, and a short duct originating from the juncture. Length of right spermatheca of IX (measured from base of ampulla to pore) = 2.44 mm. A single pair of large genital seta follicles in VII, each ligamented to the body wall, and passing through a pair of small glands prior to entering the parietes. The setae fairly short, with regular scalloping as for the genus.

***Taxonomic notes, Ingham specimens***

Large, bulbous gizzard, in V; considerable dilatation of the oesophagus in XI–XII. Nephridial tufting absent, ducts in a single series, well above *d* lines. Nephridial bodies apparently infected with nematodes coiled within the tubules. Penisetal follicles very large, conspicuous; setae long, somewhat sinuous, with fine spines towards ectal end. Spermathecal ampulla and diverticulum fused together lengthways (diverticulum slightly shorter and wider) to form a composite long-ovoid organ, surmounted by a short duct. (Ampulla



Figs 11, 12, *Diploptrema athertonii* sp. nov., Holotype. 11, genital field; 12, right spermatheca of IX.

### Remarks

There seems little doubt that the Ingham specimens are conspecific with the typical forms. There is very good agreement in most aspects, including the mutual possession of genital seta glands, very similar penial setae, and close resemblance in spermathecal construction. *D. armifera* appears to encroach upon the central portion of the *D. heteropora* domain, and is known to be sympatric with this species in the Ingham area.

The affinities of *D. armifera* are uncertain; in lacking anterior nephridial tufting, and in possessing calciferous gland-like elaborations in the oesophageal region, it does not appear to be a close relative of *D. heteropora*; the structure of the penial setae and spermathecae in the two species is also dissimilar. In many respects, *D. longiductis* (a more southern species) is close, but again, there are discrepancies with regard to the latter two characters.

Waterfall Creek, the site of the typical population, has its origins in the Mt Spec area of the Seaview range. It seems likely that *Diploptrema armifera* extends at least into the foothills of the range, though probably restricted to the surrounds of perennial streams, e.g. Insulator, Mosquito, and Gap Creeks. An immature specimen collected from the Jourama National Park, to the west, may be referable to *D. armifera*. Clearly considerably more collecting is necessary before the range of the species can be determined with any accuracy.

### *Diploptrema athertonii* sp. nov.

(Figs 11, 12)

**TYPE LOCALITY:** N Qld, 17°17'S 145°34'E, near the curtain fig tree, 12 km from Yungaburra, on the Atherton Tableland; in basaltic soil in upland complex notophyll vine forest. Coll. G. Dyne and D. Lambert, 9 Feb 1975.

**HOLOTYPE:** QMGH 2919.

**PARATYPE:** QMGH 2920.

### Description

Length 55, 52.2 mm. Width (midclitellar) 3.3, 3.1 mm. Segments 225, 230 (H, P1). Form circular in cross-section throughout, pigmentless whitish-buff in alcohol. Prostomium prolobous. First dorsal pore 10/11 (9/10 in P2). Setae 8 per segment, ventral setal couples present in XVIII; those of XVII and XIX modified as enlarged penial setae, conspicuously protruding from the body wall in many specimens; ventral couples in X modified as genital setae. Nephropores not externally recognisable. Clitellum not developed. Male pores are small orifices slightly lateral of *b* lines, far

and diverticulum internally separated by a thin partition). Prostates highly coiled in three planes, though restricted to the segments of origins causing the adjacent septa to bulge. Genital seta follicles present in VIII, flanked by a pair of whitish glands.

presetal, near intersegment 17/18, though in XVIII. Seminal grooves not demonstrable. Prostatic pores 2 pairs, coincident with penial seta openings, on raised mounds in XVII and XIX, the posterior pair somewhat smaller than the anterior. Genital markings a large segmental tumescence associated with the genital setae present in X (extending beyond *b* lines) (H, P2); a smaller intersegmental pad (confined to *bb*) present in 13/14 (H, P1, P2), and a further, small, rounded marking equatorial in 14/15 (H, P1, P2 with a like marking in XV); a series of 3 rather faint intersegmental markings with tumid posterior margins, present in 19/20 (P2), 20/21 (P1, P2), and 21/22 (P1, P2), extending laterally approximately to *b* lines. (H has all three). Female pores immediately anterior to *b* setae in XIV (on the anterior lip of the posterior intrasegmental furrow); spermathecal pores not obvious, in *b* lines, in 7/8, 8/9.

Septa 5/6 slightly thickened, 6/7 moderately so, 7/8 strongly muscularised, 8/9 moderate, 9/10 weak, remainder diaphanous. Dorsal blood vessel single; last hearts in XIII (those in XII the largest due to blood engorgement); commissurals not apparently enlarged as hearts in X and XI; those of XII and XII latero-oesophageal. Supra-oesophageal vessel seen only in the latter 2 segments (poorly developed in XI?), where it is paired intrasegmentally. Gizzard large, globular, and thickly muscularised, in V; oesophagus short, well-vascularised, and with a series of sessile, ventro-lateral calciferous glands, or vascular dilatations, in X–XIV, which are produced into thin-walled, digitiform projections, particularly in the posterior segments; the latter have distinct internal lamellae, and arise from thickened areas on the oesophagus. Intestine commences abruptly in XVI, segments XII–XVI much compressed; dorsal typhlosole commences in XXII. Holonephric, astomate, avesculate nephridia present throughout; the ducts enter the parietes in *cd*, and are thereafter not traceable. Nephridial tufting in the pharyngeal region lacking. Holandric; 2 pairs medium-large, iridescent sperm funnels in X and XI; seminal vesicles a single, large pair with conspicuous loculi, in XII. (In P2 whitish ?seminal vesicle masses were observed in IX). Prostate glands 2 pairs of flattened, tortuous tubes, the anterior pair the larger, and extending posteriad to XXII, as does the posterior set; ducts fairly short and thin-walled, and associated with very obvious penisetal follicles

in XVII and XIX. The latter are attached by slender ligaments to the dorsal aspect of the body wall; the setae gently curving, entire, though the distal  $\frac{1}{5}$  has a somewhat serrated appearance and with conspicuously spatulate tip, length of mature seta 1.71 mm; midshaft diameter 53  $\mu$ m (mean of 3). Ovaries, consisting of small clusters of oocytes, together with small funnels, seen in XIII. Spermathecae 2 subequal pairs, each consisting of a fairly long, clavate ampulla (the ental region expanded into a bulb), and a sac-like diverticulum joining the stalk of the ampulla ectally, near the origin of the short duct. (Some specimens, e.g. P1, with smaller, ?immature spermathecae, have a more tubular ampulla, and less discrete diverticular sac). Genital seta follicles present in X, no associated glands noted; the setae fairly short, ornamented over the ectal half with regularly disposed, distally directed teeth and shallow, intervening grooves that undercut the former; length of mature seta 1.03 mm; midshaft diameter 28  $\mu$ m (mean of 2); length right spermatheca of IX 1.9 mm.

### Remarks

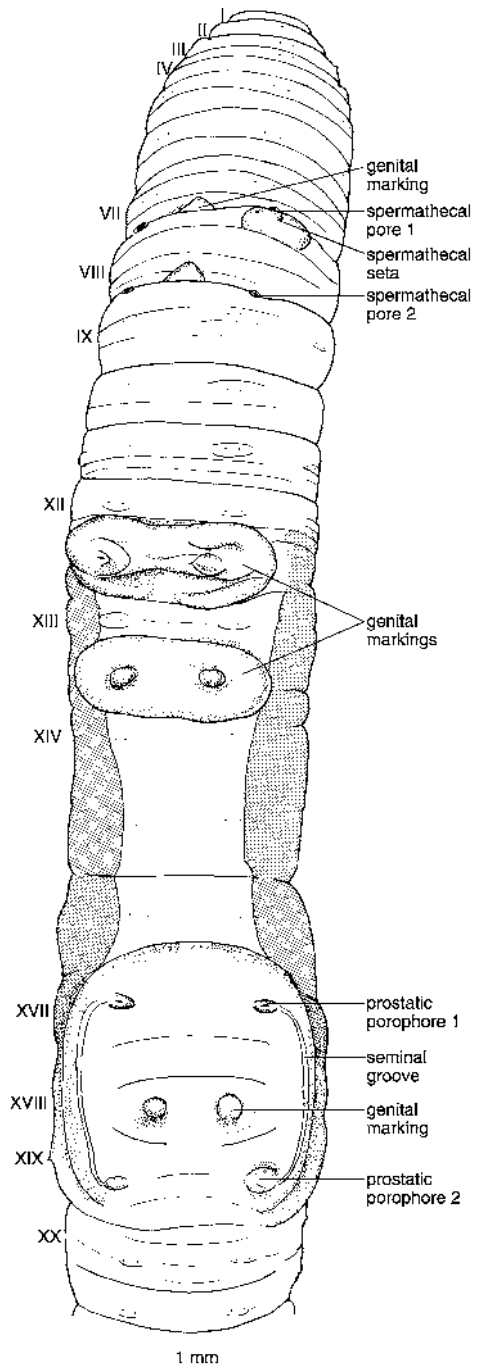
*Diploptrema athertoni* is readily diagnosed by the alignment of the genital openings with *b* lines, the proximity of the male pores to 17/18, and the presence of genital setae in X. In many respects, including the shared possession of sac-like gut diverticula, flattened, spatulate tips of the penial setae, and similar spermathecae, this species is reminiscent of the microscolecin *D. glandifera*; a shared common ancestry is suspected. Although *D. athertoni* is known to exist sympatrically with *D. bidiverticulata*, the two species are not morphologically close. The isolated forest remnants of the Atherton Tableland, and their associated faunas, represent a relictual fraction of that which existed before European settlement. Palynological studies have shown, moreover, that far from being static, vegetation types have changed dramatically, even within the 60,000 years B.P. A changing mosaic of retreating and advancing forest types, and their inherent microhabitats, would be conducive to earthworm speciation, particularly in the case of less motile forms (such as *Diploptrema*). Due to the scale of habitat destruction, unfortunately, it may never be possible to reconstruct fully the patterns of earthworm diversity on the Tableland.

***Diplootrema attenuata* Jamieson, 1997**

(Figs 13–15)

***Diplootrema attenuata*** Jamieson, 1997: 237–241, figs 5–8, 39.**TYPE LOCALITY:** Qld, Peach Creek, McIlwraith Range, 13°44'17"S 143°20'15 ±5"E, altitude 500–520 m in bank of stream in notophyll vine forest, on Kintore adamallite granite. Coll. K.R. McDonald, A.J. Stewart, W.E. Martin, 26 Sep 1995 and, K.R.Mc., A.J.S., 23 Sep 1996.**HOLOTYPE:** QM G212000 (includes microscope slides of left and right anterior penial seta and left genital setae of VIII).**PARATYPES:** 1–8 QM G212038–45; P9 QM G212046; P10–12 QM G212019–212021; P13–17 QM G213386–213390; P18–20 QM G211972; P221–23 QM G213402–213404.**OTHER MATERIAL:** Several specimens not designated types QM G211980, 212022.**Description (after Jamieson, 1997)**

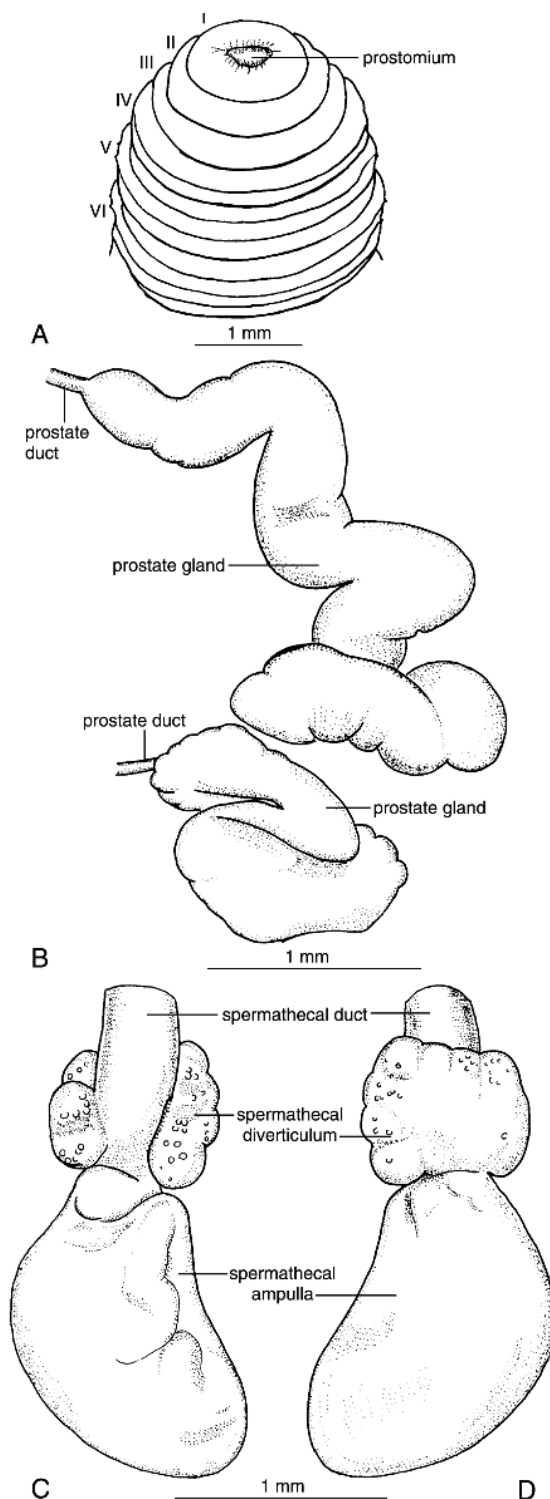
Length 106–163 mm (a live specimen 230 mm). Width (midclitellar) 2.0–2.5 mm. Segments 140–256. Uniformly circular in cross-section throughout. Pigmentless buff in alcohol, clitellum, when tumid, pale pink; in life, blood red throughout. Prostomium small, prolobous, slightly indenting the peristomium which is about as long as segment II. Dorsal pores absent. Setae 8 per segment, commencing on II; ventral setal couples absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital setae present in VIII, with the usual diplootreman ornamentation consisting of notches.  $aa: ab: bc: cd: dd = 4.8: 1.0: 4.3: 0.8: 11.6; = 16.8: 3.5: 15.1: 17.9: 40.5\%$ . Nephropores not visible. Clitellum well developed, saddle-shaped, extending over  $\frac{1}{2}$ XII–XVII, with a midventral gap that extends to, or slightly beyond, *b* lines. Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a minute oval papilla which is equatorial and slightly lateral of *b* lines relative to adjacent segments; the papillae of a side linked by a weakly developed slightly parenthetic seminal groove; the entire male genital area forming a raised, almost square area, slightly longer than wide, with rounded vertices. Genital markings: a broad, unpaired midventral pad extending laterally beyond *b* lines, intersegmental in some of 10/11, 11/12, 12/13, 13/14, 14/15, but extending almost to the setal arcs of each adjacent



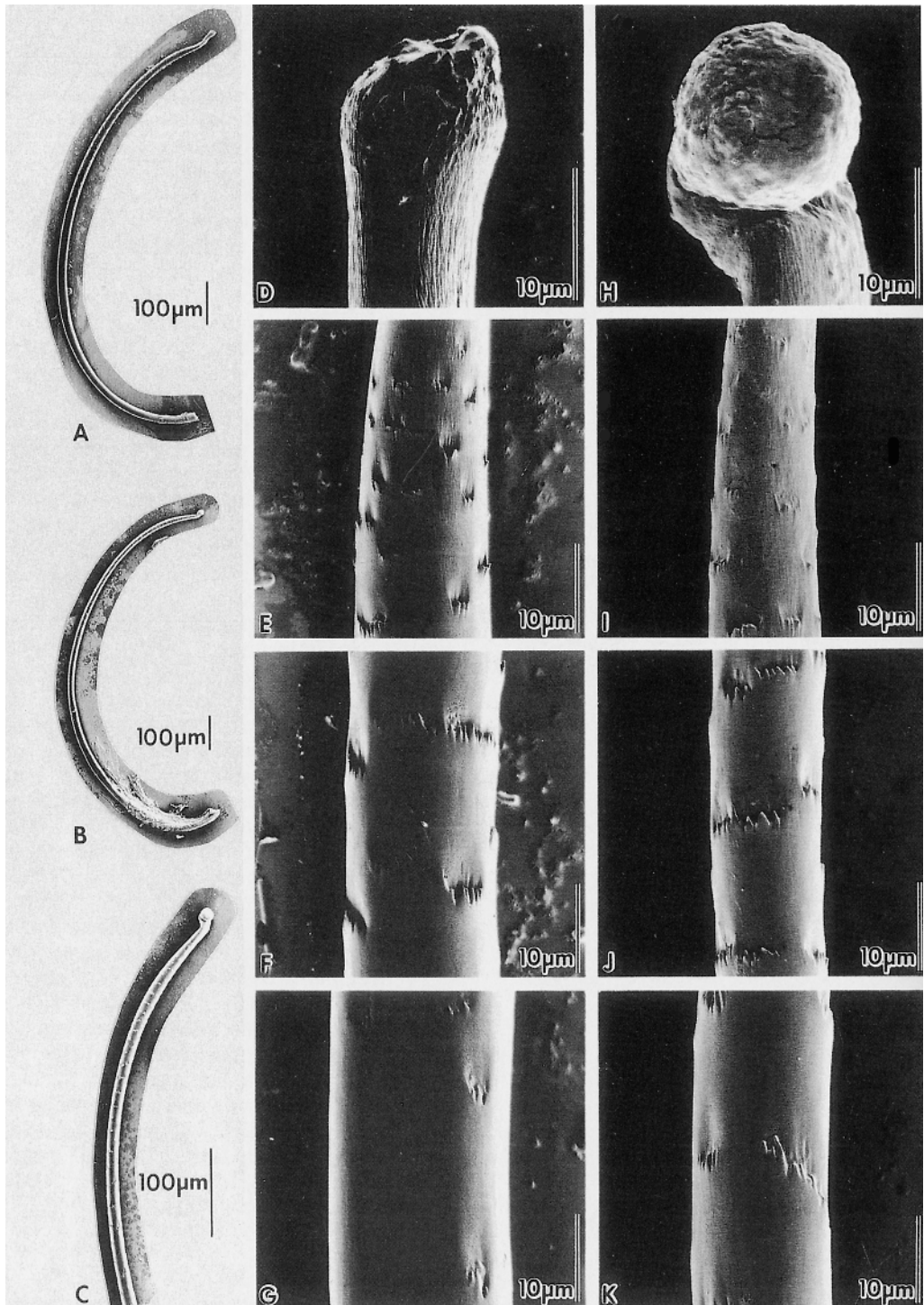
**Fig. 13.** *Diplootrema attenuata* Jamieson, 1997, genital field of Holotype. [After Jamieson 1997]

segment; each pad bearing a pair of approximately hemispheroidal papillae median of *a* lines; highly diagnostic is a similar pair of papillae, on a less distinct transversely oval area, segmentally situated on XVIII (all specimens); a transverse segmental pad frequently present in XX. Further markings typically a midventral postsetal triangular slight tumescence in VII and VIII. An unpaired oval-rectangular genital tumescence on the left side straddling and extending beyond *ab*, in the anterior half of VIII, with two punctuations representing genital setae. Female pores small transverse slits presetally in *a* or *b* lines. Spermathecal pores 2 pairs, in 7/8 and 8/9, slightly lateral of setae *b*; inconspicuous but definite orifices visible by parting the intersegment.

Septa 5/6–8/9 strongly thickened, the last two the thickest. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in X–XIII, latero-oesophageal, with connectives to the dorsal and supra-oesophageal vessels; commissurals in IX anteriorly slender, not heart-like, though in IX, at least, possibly latero-oesophageal. Gizzard small, compressible though with some muscular sheen, almost vestigial, in V. Oesophagus suppressed in VI by backward extension of septum 5/6; segmentally slightly swollen, and vascularised in VII to IX; a simple tube from X(?), XI to ½XIX in which the intestine commences with abrupt expansion; typhlosole absent. Ventrolateral masses in XIII give the spurious impression of calciferous glands but are not connected to the oesophagus and disintegrate on manipulation. Holonephric throughout; nephridia not seen in a few anterior segments and no tufting detected; nephridia with preseptal funnel near nerve cord and slender duct discharging in line with the dorsal setal couples (*cd*); caudally the body of the nephridium has the appearance of a convoluted sac but bladders are absent. Holandric; large sperm masses, and very large iridescent sperm funnels free in X and XI. Two pairs of large, racemose seminal vesicles which fill the length of their segments, in XI and XII. Moderately large, flattened bushy ovaries, and funnels, in XIII; small, multichambered, berry-like masses on each side of the oesophagus in XIV are presumably ovisacs. Prostates two pairs, with ducts discharging in XVII and XIX; those in XVII considerably the larger and with the form of tortuous thick tubes that end in XVIII; those in XIX flattened and strap-like in their midregion, and approximately S-shaped; each



**Fig. 14.** *Diploptrema attenuata* Jamieson, 1997, Holotype: **A**, prostomium; **B**, right prostates—right penial setae omitted; **C**, left spermatheca, ventral; **D**, left spermatheca, dorsal. [After Jamieson 1997]



**Fig. 15.** *Diploptrema attenuata* Jamieson, 1997, Paratype, scanning electron micrographs: **A** right penial seta of XVII; **B** and **C**, a right penial seta of XIX; **D–G**, appearance of a seta shown in **A**, from the tip to near the base; **H–K**, same for seta shown in **B** and **C**. [From Jamieson 1997]

prostate with a short slender duct which is obscured by the large penisetal follicles. Male genital field of XVII–XIX represented internally by diffuse glandular modification of the body wall but no bursae present. Paired, conjoined vasa deferentia with closely adpressed bends, and spermatozoal iridescence, traced on each side to immediately behind the ectal end of the duct of the anterior prostate, but termination not seen. Penial setae strongly curved throughout their lengths; the tip not widened, reflected dorsally or not and ending bluntly in a rounded swelling with a pitted surface; sculpturing (best developed in the midregion) consisting of pointed scales, contiguous side by side, in incomplete circlets; the circlets spaced longitudinally at approximately 15 µm intervals; the scales stopping short of the modified tip near which they are in small groups rather than circlets; length of a well-developed right penial seta 1.3 mm (P10). Genital setae present at the tumescences in VIII; each with the usual diploptreman appearance, a stout seta with four opposed longitudinal series of long notches and the tip slightly expanded below the terminal point; length left seta = 0.5 mm (incomplete?); greatest width, near base, = 25 µm. Spermathecae 2 pairs, the posterior somewhat the larger, each with a large irregularly ovoid ampulla and straight broad, well-demarcated muscular duct of about half its length; a multiloculate diverticulum, with a form reminiscent of a clenched fist, sessile dorsally on the duct at the junction of the latter with the ampulla, the few main loculi being laterally situated and filled with innumerable very small, iridescent sperm balls; length left spermatheca of IX = 2.3 mm; length ampulla = 1.4 mm; ratio length spermatheca : length duct = 2.6; greatest dimension of diverticulum (transversely) = 0.8 mm.

### Remarks

The genital field, particularly the two knob-like genital markings median to the seminal grooves on segment XVIII, is diagnostic of *D. attenuata*. The male genital field of this species, when fixed, is emphasised by the fact that the body is almost always dorsally arched anteriorly and posteriorly to it. The body is also contorted elsewhere.

The absence of dorsal pores is attributable to an amphibious existence in earthworms. It is unknown in other published species of *Diploptrema* with the exception of *D. cornigravei* (Michaelsen, 1907) and possibly *D. macleayi* (Fletcher, 1890), both species only described briefly from Western and North Western Australia, respectively.

### *Diploptrema australis* (Michaelsen, 1889)

(Figs 16, 17)

*Acanthodrilus australis* Michaelsen, 1889: 9–12, fig. 2.

*Notiodrilus australis*; Michaelsen 1900: 137.

*Diploptrema australis*; Jamieson and Dyne 1976: 450.

**TYPE LOCALITY:** Qld, Cape York Peninsula.

**HOLOTYPE:** HM V398 (re-examined).

**PARATYPE?:** '*Acanthodrilus australis* Michaelsen and Pickford', USNM #020979. South Pacific Ocean; Cape York. Donated Pickford. ALC + 1 slide = *Eodrilus australis*.

### Description (after Michaelsen 1889; Jamieson and Dyne 1976)

Length 60–140 mm. Width 4.5–6 mm. Segments 109–443. Brownish. Prostomium not clearly visible. First dorsal pore 12/13. Setae closely paired. Nephropores far dorsal of *d*. Female pores in XIV, shortly anterolateral to setae *b*. Clitellum saddle-shaped, XIII–XIX. Prostatic pores, equatorial in XVII and XIX, on small but conspicuous papillae in setal lines *ab*. Accessory genital markings paired tubercles in 11/12, 12/13, and 20/21; the first lateral to, the last almost over setal lines *b*. Spermathecal pores two pairs, on eye-like papillae, in 7/8 and 8/9, in *ab* or (re-examination) *b* lines.

Gizzard in VI. Calciferous glands absent. Testes and funnels free, in X and XI. Seminal vesicles in IX, XI and XII. Bushy ovaries and their funnels in XIII. Prostates, in XVII and XIX, very long, much coiled. Genital setae absent. Penial setae 2.4 mm long, strongly curved; widened above the curve, before the slightly recurved tip, on the concave side of the bend, spoon-shaped; at the extreme end with fine striations. Spermathecae in VIII and IX; adiverticulate but with sperm chambers in the wall (Michaelsen 1889, 1900b) or diverticulum multiloculate, large though smaller than ampulla (Jamieson and Dyne 1976).

### Remarks

*Diploptrema australis* is diagnosed by a combination of characters: presence of accessory genital markings as paired tubercles in 11/12, 12/13, and 20/21; the first lateral to, the last almost over setal lines *b*; absence of genital (as distinct from penial) setae; holandry, with seminal vesicles in IX, XI and XII; absence of calciferous glands; and location of nephropores far dorsal of *d* lines.

***Diploptrema bidiverticulata* sp. nov.**

(Figs 18, 19)

**TYPE LOCALITY:** (1) Qld, 17°17'S 145°34'E, near the curtain fig tree, 12 km from Yungaburra, on the Atherton Tableland, in rocky basaltic soil in upland complex notophyll vine forest. Coll. G. Dyne and D. Lambert, 9 Feb 1975.

**PARATYPE LOCALITIES:** (1) As above. (2) Qld, 17°25'S 145°31'E, 16 km south of Atherton, on Herberton Road, in complex notophyll vine-forest. Coll. G. Dyne and D. Lambert, 8 Feb 1975.

**HOLOTYPE:** (1) QMGH 2901.

**PARATYPES:** (1) QMGH 2902, ANIC GD.95.2.2 (5 immature).

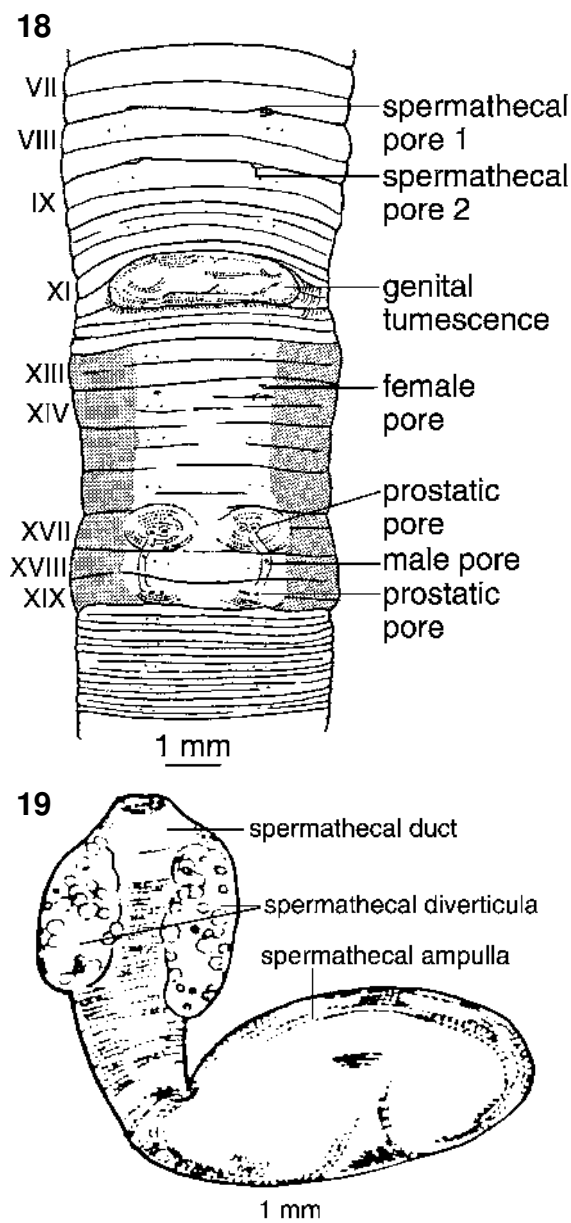
**Description**

Length 96.5, 78.5 mm. Width (midclitellar) = 4.4, 5.3 mm. Segments 229, 231 (H, P1). Uniformly circular in cross-section throughout; pigmentless buff in alcohol, clitellum pinkish-brown. Prostomium prolobous?, first dorsal pore in 10/11. Setae 8 per segment, ventral setal couples of XVIII present, those of XVII and XIX enlarged as penial setae, though only those on left XIX conspicuously protruded in H. Genital setae absent. Nephropores visible as small, whitish dots intersegmentally, in the clitellar region, slightly dorsal of *d* lines. Clitellum well developed, tumescent, saddle-shaped over segments XIII–XIX, extending to *b* lines in the midventral region; dorsal pores and most intersegmental furrows are obscured dorso-laterally. Male pores minute, slightly pre-setal, and just lateral of *b* lines in XVIII; they lie in shallow, ill-defined seminal grooves that join the prostatic pores of a side. The latter are associated with the peniseta pores, and situated equatorially in XVII and XIX, atop raised mounds. Genital markings a single, large tumid pad, broadly central in 11/12, and extending laterally to mid *bc*; the pad consists of (H) a central raised region demarcated by a circumferential furrow, and is present in all specimens examined (mature). No other markings distinguishable. Female pores a pair of tiny openings, presetal in *ab* (nearer to *a*), in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, on small papillae.

Septa 5/6 moderately thickened, 6/7–9/10 strongly muscularised, 8/9 perhaps the thickest; 10/11, 11/12 only slightly thickened, remainder thin. Dorsal blood vessel single; last hearts in XIII, those in X–XIII latero-oesophageal: connectives from the dorsal vessel are extremely thin (?functional); supra-oesophageal vessel extends to XIV, anterior origin uncertain. Gizzard large, and barrel-

**Figs 16, 17, *Diploptrema australis*, Michaelsen, 1889.**  
**16**, genital field and (left) penial seta; **17**, genital field, HM V398. [16, from Michaelsen 1889; 17, original]





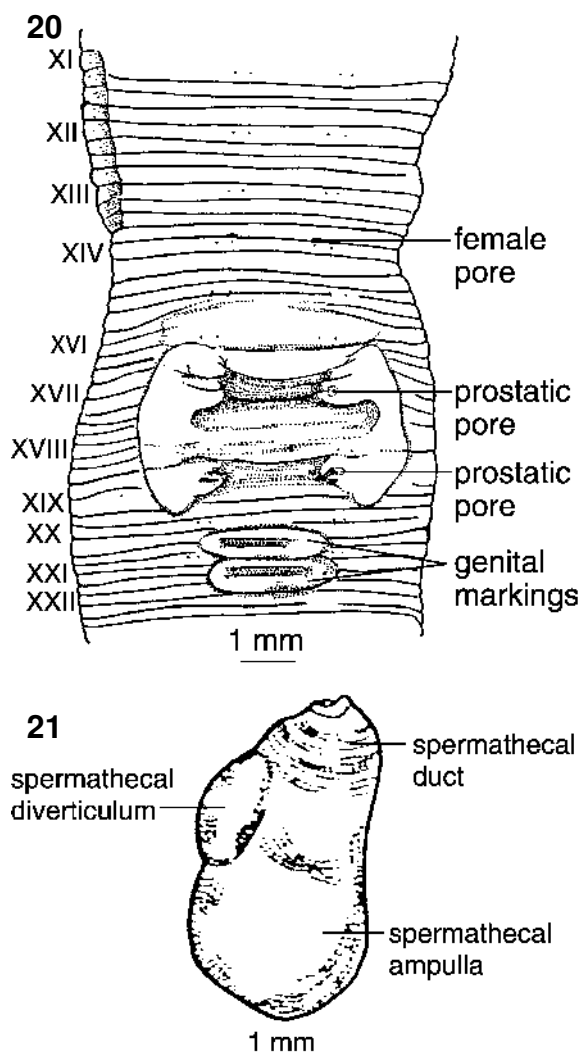
**Figs 18, 19.** *Diplotrema bidiverticulata* sp. nov., Holotype. 18, genital field; 19, right spermatheca of IX.

shaped, in V, with expanded anterior rim (=proventriculus); oesophagus compressed anteriorly (by posteriad expansion of the gizzard), moderately vascularised and thin-walled in VI–XVII; pouching or calciferous development lacking. Intestine commences with sharp demarc-

ation in XVIII, dilates rapidly, and attains maximal width in XX; a single, low, dorsal typhlosole commences in XX. Ingesta: very fine organic material mixed with reddish soil particles. Holonephric, the stomate, avesculate bodies confined on the body wall between setal lines *b* and *c*. Ducts very thin and delicate, only occasionally demonstrable, apparently entering the parietes through *d* lines (note: externally, nephropores seen dorsal of *d*) Pharyngeal tufting absent. Holandric: 2 pairs medium-sized, iridescent spermatic funnels imbedded in densely coagulated ?sperm masses in X and XI; 2 pairs small, rounded seminal vesicles detected in IX and XII, consisting of small, tightly packed loculi. Prostates 2 pairs of tortuous tubular organs restricted to XVII and XIX, the anterior pair by far the larger; ducts thin and rather short. Penisetal follicles conspicuous, the individual follicles of a pair conjoined, attached to the dorsal aspect of the body wall by obvious ligaments that pass through the prostatic coils; the setae fairly short, strongly arcing, with faint toothing giving a slightly serrated appearance to the distal  $\frac{1}{5}$ , tip straight; length of mature seta 1.47 mm; midshaft diameter 28  $\mu$ m (mean of 3). Ovaries large, consisting of several oocytic sheaves on each side, together with large, plicate oviducal funnels, in XIII; ovisacs not demonstrable. Spermathecae 2 subequal pairs in VIII and IX, each a bent organ consisting of an ental ampullal sac, a fairly long, muscular duct which dilates ectally, and a pair of sessile diverticula located at each side of the expanded terminal portion of the duct; copious diverticular iridescence suggests amphimictic reproduction for this species. In situ, the ampullae of the spermathecae tend to be reflected anteriorly through the septum of the adjacent segment. Length of right spermatheca of IX 3.5 mm. Genital setae lacking.

### Remarks

Differences between the Herberton Road and typical populations appear to be slight: in the former, the spermathecal ampulla is apparently provided with a terminal bulb, the seminal vesicles of IX are larger, and are composed of more robust loculi, and segment XI is encapsulated by dorsal outgrowths of the surrounding septa (a condition commonly seen in north Queensland *Diplotrema* species, and possibly a testis-sac equivalent). The species as a whole is readily distinguished from its congeners by the possession of a duplicated spermathecal diverticulum (rare in *Diplotrema*, seen also in *D. boardmani* and *D. cornutheca*) together with details of the genital apparatus, including the absence of genital setae.



**Figs 20, 21, *Diploptrema bifistularis* sp. nov.** 20, genital field of Holotype; 21, right spermatheca of IX, Paratype 1.

***Diploptrema bifistularis* sp. nov.**

(Figs 20, 21)

**TYPE LOCALITY:** (1) Central E Qld, 23°22'S 150°32'E, 29 km south of Rockhampton, near Bruce Highway, in heavy, black soil. Coll. C. Horan, 22 Dec 1969.

**PARATYPE LOCALITIES:** (1) As above. (2) Central E Qld, ca 22°49'S 149°53'E, approximately 3 km south of Marlborough, in sandy soil under dry grass. Coll. C. Horan, 8 Dec 1969.

**HOLOTYPE:** (1) QMGH 2940.

**PARATYPES:** (1) QMGH2941 (paratypes 1–3); (2) Paratypes 4 and 5, lodgement unknown.

**Description**

Length 150, 110+ mm (posterior amputee). Width 6.2, 6.0 mm. Segments 230, ? (H, P1). Uniformly circular in cross-section throughout, pigmentless buff in alcohol, prostomium prolobous. First dorsal pore 11/12. Setae 8 per segment, not prominent, in regular longitudinal rows throughout; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae, those of VIII and IX replaced by modified genital setae nephropores visible, particularly in the clitellar region, as very small, intersegmental papillae, in line with mid-*cd*, or, more usually, closer to *d* lines. Clitellum undeveloped in all otherwise sexually mature specimens examined. In the Holotype, there is some slight evidence of clitellar tissue over segments XVI–XIX, but this is not definite. Male pores not certainly demonstrated, but presumably lying in mid-XVIII, in the shallow, poorly defined seminal grooves joining the prostatic porophores. Male field roughly quadrangular, with raised lateral rims (on top of which run the seminal grooves), and tumid posterior margin; the central depression is bisected by a wide, raised, median strip running transversely. The prostatic porophore mounds project into the central concavities of the male field from the corners of the latter; each porophore opens confluent with a conspicuously projecting penial seta, with 2 setae occasionally present. Female pores a pair of slits seen presettally, in *a* lines, in XIV. Spermathecal pores 2 pairs, in 7/8, 8/9, approximately aligned with *b* setae. Accessory markings a series of median, unpaired, broadly elliptical markings in 20/21 and 21/22, each with an inner broad ellipse of distinct glandular tissue (H, P1, P3); a similar marking sometimes present in 15/16 (?H, P1, P2); genital setae tumescences absent.

Septa 5/6, 6/7 moderately thickened, 7/8–12/13 much augmented with musculatures 13/14 and posterior septa diaphanous. Dorsal blood vessel single posterior to 13/14 (or deeply grooved), where it undergoes contortion and separation; in XII it is clearly bifurcate, and continues to bifurcate intrasegmentally in more anterior segments (the 2 vessels rejoining intersegmentally), resulting in a looped appearance; dorsal vessel single; in and anterior of V, continuous onto the pharynx. Last hearts in XIII; other large, heart-like commissurals restricted to X–XII; all have thin connectives from the dorsal vessel, and more substantial ones from the supra-oesophageal vessel. Remaining commissurals diminishing in size anteriorly, to VI, and dorsoventral only. Supra-oesophageal vessel seen

in VII– $\frac{1}{2}$ XIV, adherent to the roof of the oesophagus. Gizzard small-medium in size, in V, with a distinct muscular sheen, though readily compressed; a prominent anterior rim (=proventriculus) present; oesophagus moniliform (constricted intersegmentally), and lacking excrescences, in VI–XVI; intestine commencing abruptly in XVII, muscular thickening or typhlosome absent. Stomate, avesculate holonephridia predominantly present, the small, preseptal nephrostomes usually in *ab*; ducts traceable to *cd*, where they enter the parietes presetally; nephridial bodies in II–V with complex elaboration of tubules (?tufted), those in III the largest, their ducts not traceable; remaining nephridia comparatively simple: larger and more highly coiled in the oesophageal region, less so in the intestinal region. Holandric; 2 pairs small, plicate, non-iridescent spermathecal funnels seen in X and XI, and 2 subequal pairs of conspicuously loculate seminal vesicles adherent to 10/11 and 11/12 in XI and XII. Vasa deferentia only spasmodically demonstrable on the body wall. Prostate glands 2 pairs of simple, tubular structures restricted to XVII and XIX, their ducts short and only slightly muscularised. The latter associated with conjoined peniseta follicles, containing 8–10 reserve setae in various stages of growth; cross-banded copulatory musculature involving the follicles and the body wall in segments XVI–XIX, well developed. The setae relatively short, gently curving; the distal  $\frac{1}{2}$  of the shaft is ornamented with regularly spaced, though incomplete, circlets of minute, jagged teeth; the tip, which is acuminate, is free of the latter; length of mature seta 2.04 mm (mean of 3); midshaft diameter = 14  $\mu$ m. Small ovaries and modest, diaphanous funnels present in XIII; ovisacs absent. Spermathecae 2 pairs, in VIII and IX, discharging anteriorly in their segments; each a simple sac, with the ampulla, diverticulum and duct barely distinguishable: the ampulla is bulb-like, the duct short and wide, and the diverticulum appears more or less a small protuberance on one side of the latter. Diminutive genital seta follicles present in VIII–X, each with a small number of short setae, embedded in a glandular matrix; the setae quite stout, straight, and tapering rapidly from the broad base to a rather fine tip, ornamented with concave scalloping over the distal  $\frac{1}{3}$ ; length of mature seta 0.61 mm; midshaft diameter 27  $\mu$ m (mean of 3).

#### Remarks

Worms from the Marlborough locality differ from those of the type locality as follows: they have a larger, more muscular gizzard, have the seminal vesicles in IX and XII, and in one specimen, lack the genital seta follicles of X. These are comparatively minor differences, particularly in

view of a convincing similarity in genital fields, and the mutual possession of a bifurcate dorsal blood vessel. Allied species include *D. boardmani* (from near Gladstone) and *D. bulburrensis*. The adaptability of the genus is evident if one compares the habitat of the latter species (rainforest) with that of *D. bifistularis* (grassland, subject to prolonged dry seasons).

#### *Diplotrema biloela* Blakemore, 1997

*Diplotrema biloela* Blakemore, 1997: 1792–1794, fig. 2.

**TYPE LOCALITY:** Qld, 24°24'S 150°31'E, Biloela; adjacent to the QDPI '135' agricultural research site, dug from the clay banks of Callide Creek under organic soil horizon.

**HOLOTYPE:** RB.94.5.1 (ANIC).

**PARATYPES:** P1 RB.94.5.2 (ANIC); P2–4 RB.94.5.3 (ANIC).

#### Description (after Blakemore 1997)

Length 60–70 mm. Width ca 3 mm. Segments ca 95 (difficult to discern owing to small setae and deep secondary annulation). Colour unpigmented, the anterior pink in life. Prostomium proepilobous. First dorsal pore 6/7 (or 7/8?) continuous on clitellum. Setae 8 per segment from II, retained on XVIII, small and closely paired (*ab* and *cd* same width); genital setae small on VIII, larger on IX; penial setae enlarged (red coloured) on XVII and XIX. (Ratio on XII, mean of two 10: 1: 5: 1: 15: 0.35). Nephropores in *cd* line. Clitellum XIII–XVII, tumid and annular but interrupted ventrally by male field. Male pores minute in XVIII lateral to *ab* line near seminal grooves between pairs of prostatic pores in XVII and XIX. Genital markings none but genital setae on paired raised tumescences on (VII), VIII and IX. Female pores minute anterior on XIV. Spermathecal pores 7/8 and 8/9 small in *ab* lines.

Septa 5/6–7/8 membranous. Dorsal blood vessel doubled from VI as circular intrasegmental loops that reunite at septa, from XIII loops more elongate. Hearts, in X–XIII, connect with ventral vessel. Gizzard strongly muscular, cup-shaped in V but displaced posteriorly on elongate (over 10 mm long) pharynx which is tortuous in IV. Extended pharynx contains mainly dark, woody organic matter, comminuted after passage through the gizzard. Calciferous glands absent. Intestine from XVII, typhlosome not detected to about XXV. Nephridia convoluted tubular holonephridia from V, avesculate and discharging in line with the lateral setal couples; anterior tufted nephridia not found. Male funnels in X and XI, enveloped

in large sacs that encompass nephridia and oesophagus and are distended with white (seminal?) coagulum; seminal vesicles conspicuous on anterior septum of XII (coagulated annular mass surrounding oesophagus in IX possibly also seminal but not connected to 'testis-sac'). Ovaries small in XIII. Prostates two pairs, convoluted tubular, with short muscular ducts in XVII and XIX, [the glands?] confined to their segments, anterior pair larger; ensheathed penial setae [not described] converge near each prostatic pore. Ventral body wall in this region not glandular. Spermathecae 2 pairs in VIII and IX; ampulla spherical, tapering to duct with equally large round diverticulum; the anterior pair only slightly smaller.

### Remarks

*Diploptrema biloela* is here considered closest to *D. tyagarah* Dyne (1979b), although the genital and penial setae, not described by Blakemore (1997), cannot be compared. It differs notably from *D. tyagarah* in lacking genital markings, other than those of the genital seta glands. Further unusual features, noted by Blakemore, are the 'testis-sacs', the greatly extended pharynx and the looped pairing of the dorsal blood vessel (but see *D. queenslandica* below).

### *Diploptrema boardmani* sp. nov.

(Figs 22, 23)

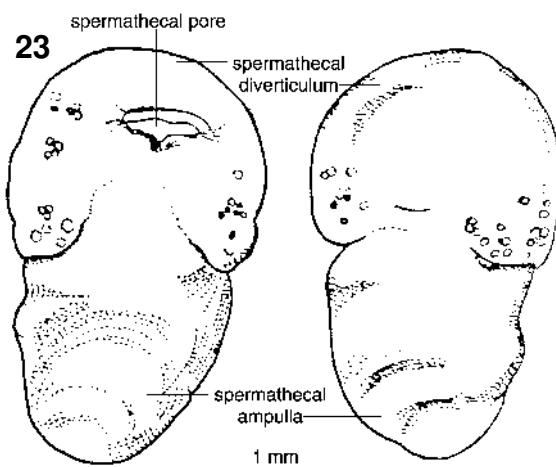
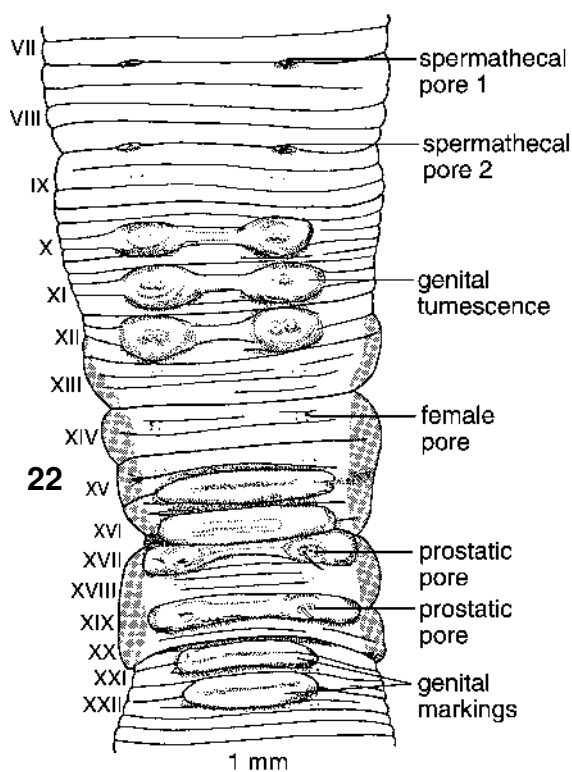
**TYPE LOCALITY:** Central E Qld, ca 23°52'S 151°15'E, creek bank, approximately 3.2 km out of Gladstone. Coll. W. Boardman, Jul 1929.

**HOLOTYPE:** AM W17881.

**PARATYPES:** (14 specimens) AM W17882–17895.

### Description

Length 101, 144 mm. Width (midclitellar) 6.5, 6.4 mm. Segments 165, 205 (H, P1). Body uniformly circular throughout, though strongly constricted intersegmentally in the clitellar region, pale biscuit in alcohol, clitellum brick red. Prostomium prolobous; first dorsal pore in 10/11. Setae 8 per segment, in uniform rows throughout; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of X–XII replaced by genital setae. Nephropores conspicuous in light patches on the clitellum, in a single line, running through *cd*. Clitellum very well developed and protuberant, saddle-shaped, encompassing segments ½XII–XX, deeply constricted in the intersegments, particularly those of 14/15, 16/17 and 18/19. Setae, dorsal pores obscured; clitellum not developed ventrally beyond the point *bc* from *b*. Male pores small slits slightly presetal (in an intrasegmental



**Figs 22, 23, *Diploptrema boardmani* sp. nov., Holotype.** 22, genital field; 23, right spermatheca of IX, dorsal and ventral views.

groove), lateral of *b* lines, in XVIII; seminal grooves shallow and indistinct. Prostatic porophores on raised mounds, those of a segment conjoined by a tumid band; penial setae protruding in many specimens. Genital markings 3 pairs large, tumid pads associated with the genital setae

in X–XII, conjoined across the midventral line to form fairly continuous raised bands in the above segments (present in all specimens examined with the exception of P10, in which the marking in XI is lacking); pair of median, intersegmental tumid pads in 15/16 and 16/17, extending beyond *b* lines (H, P1, P3–5, P7, P11–14) or in 16/17 only (P2, P8–10); a similar series of pads restricted to *bb*, in 20/21, 21/22 (H, P2, P9–10), some specimens with an additional marking in 22/23 (P1, P3, P5–8, P11–12), and occasionally, a marking in 19/20 (P4, P7–10), a single specimen having a pad in 20/21 (P14); 2 further, small, intersegmental markings are rarely seen, in 14/15 (P6, P11) and in 23/24 (P13). Female pores small orifices seen presetally in *b* lines of XIV. Spermathecal pores 2 pairs of obvious slits, in *b* lines, in 7/8, 8/9.

Septa 5/6 moderately muscularised, 6/7–10/11 strongly thickened, 11/12 moderately so; remainder thin. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; commissurals in X–XIII all with definite connectives from both the dorsal and supra-oesophageal vessels (the connectives received from the latter conspicuously more robust in XII and XIII); remaining commissurals smaller, and dorsoventral only; supra-oesophageal vessel seen in IX–XIV only. Gizzard fairly large and globular, in V, with a considerable portion of softer proventriculus anteriorly; oesophagus uniform in diameter throughout, in VI–XVII, lacking any elaborations; intestine commences abruptly in the latter part of XVII, a strongly developed dorsal typhlosole present after ca XXXII. Nephridia holonephric throughout, excepting segments II–V, where moderate-sized, astomate tufted clumps of nephridial bodies are present (those of II and V the largest); in the latter region, the ducts of the individual nephridia form a composite duct that apparently discharges exonephrically in a position similar to that of the mid-body nephridia. The latter are conspicuously stomate, and have a thin duct discharging in *cd*. Holandric; large, highly convoluted and brilliantly iridescent spermathecal funnels present in X and XI, with 2 large, finely acinous pairs of seminal vesicles, flecked with iridescence, in IX and XII. Prostate glands 2 pairs of rather loosely coiled, tubular organs in XVII and XIX, the anterior pair almost twice as large as the posterior set, and extending into XVIII; the prostatic ducts somewhat short and straight, and not highly muscular. The latter are associated with small penisetal follicles, supplied with a moderate amount of copulatory musculature (mostly concentrated in XVIII); the setae fairly strongly curved, into a semicircular shape; the distal  $\frac{1}{3}$  with a distinctive notched appearance due to the

presence of numerous irregularly spaced clusters of sharp, jagged teeth, that are more densely concentrated near the tip, and sparse further down the shaft. Length of mature seta 1.89 mm; midshaft diameter 22  $\mu$ m (mean of 3). Ovaries fan-shaped, with numerous developing oocytes, together with large, plicate, translucent oviducal funnels, in XIII. Spermathecae subequal, in VIII and IX, each consisting of a simple pouch-like ampulla, fusing broadly with a sessile diverticulum that surrounds the short duct. Length of right spermatheca of IX 2.86 mm. Genital seta follicles 3 pairs, in X, XI and XII, all of similar dimensions, and ligamented to the body wall; the setae gently curving, the ectal  $\frac{1}{3}$  ornamented with the deep notching characteristic of the genus. Length of mature seta 0.88 mm; midshaft diameter 24  $\mu$ m (mean of 2).

### Remarks

*Diploptrema boardmani* may be diagnosed by the number and position of the genital setae, shape of the spermathecae, and details of the genital field. It appears to be closely related to *D. bulburinensis*, a species found some distance westwards, though the latter may be distinguished by the presence of metandric gonads and rudimentary genital setae. Attempts to collect fresh material of *D. boardmani* from the environs of Gladstone have not been successful; the two possible localities deduced from Boardman's somewhat ambiguous collecting site description are now subject to considerable human interference.

### *Diploptrema bulburinensis* sp. nov.

(Figs 24, 25)

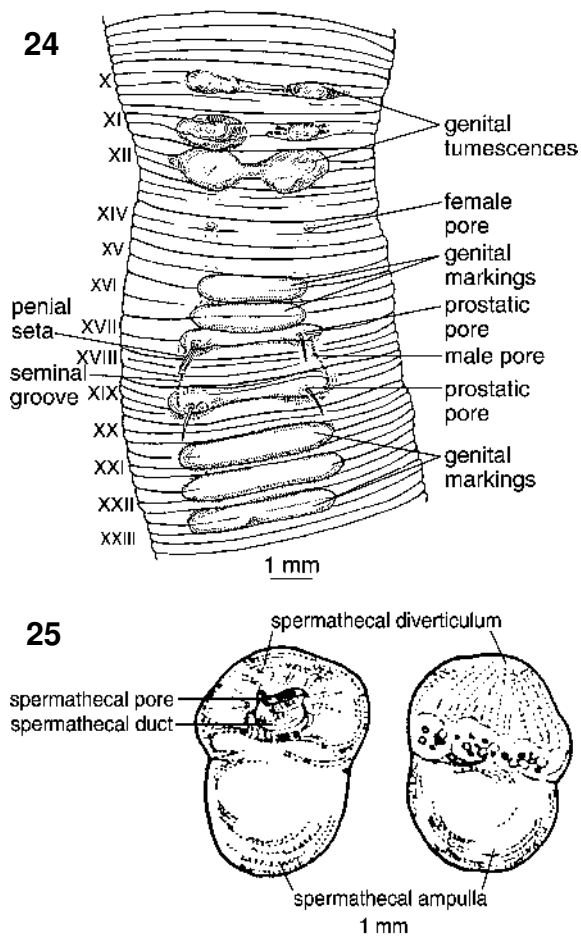
**TYPE LOCALITY:** Qld, 24°33'S 151°22'E, Bulburin State Forest, SW of Miriam Vale, in volcanic soil under rainforest. Coll. R. Raven, 26 Feb 1977.

**HOLOTYPE:** QMGH 2897.

**PARATYPES:** 2 specimens, lodgement unknown.

### Description

Length 142, ? mm. Width 6.2, 5.8 mm. Segments not determinable (H, P1 — posterior amputee). Form circular in cross-section throughout, with a midclitellar constriction, giving the forebody a bulbous appearance. Prostomium probolous; first dorsal pore 11/12. Setae *a* and *b* of XVIII lacking; those of XVII and XIX modified as enlarged penial setae; those of XII specialised as genital setae. The ventral setal couples of X and XI are somewhat enlarged, but are not true copulatory setae. Nephropores spasmodically visible as minute papillae in the intersegments of the anterior portion of the body, in *cd*. Clitellum faintly developed, its extremities not discernible. Male pores minute,



**Figs 24, 25.** *Diploptrema bulburinensis* sp. nov., Holotype. **24**, genital field; **25**, right spermatheca of IX, dorsal and ventral views.

barely recognisable in XVIII (approximately equatorial in that segment), somewhat lateral of *b* lines, in very faint seminal grooves. Prostatic porophores 2 pairs, on conspicuous mounds in XVII and XIX, apparently discharging confluent with the penial setae (several of the latter are protruding in the Holotype). Immediately posteriad of each porophore mound lies a shallow depression. Genital markings a series of broad, unpaired, intersegmental, tumid pads in 15/16 (H only) and 16/17 (H, P1) extending across *bb* and slightly beyond; similar pads present in 20/21–22/23 (H, P1), and faint 23/24 (H only); conspicuous dumbbell-shaped genital seta swellings present in XII, and to a much lesser extent, in X–XI. Female pores obvious on small, rounded papillae, in *ab* (the pore itself in line with *b*), on XIV.

Septa 5/6 moderately muscularised, 6/7–10/11 strongly thickened (7/8 possibly the strongest), septa 10/11 and 11/12 fused around the periphery to encapsulate segment XI. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; at least those commissurals in XII and XIII receive connectives from both the dorsal and supra-oesophageal vessels; the remaining commissurals are conspicuously smaller, and increase rapidly in size anteriorly. Supra-oesophageal vessel not traceable outside XII and XIII. Gizzard, large, firm and muscular, in V; somewhat short and barrel-shaped, it has a definite anterior proventriculus; oesophagus short and uncomplicated, moderately well-vascularised, in VI–XVII; intestine commencing in XVIII, a definite dorsal typhlosole present after XXVIII (approx.). Holonephridia present throughout, commencing in II; each nephridial body is conspicuously stomate, and possesses an avascular duct passing to the exterior through *d* lines. Anterior tufting lacking. Metandric; large, convoluted spermathecal funnels seen in XI only (often rupturing the septa encapsulating that segment); very large, finely acinous seminal vesicle masses present in XII only. Prostate glands approximately equi-sized tubular organs, of which there are 2 pairs, in XVII and XIX; the glands restricted to the latter segments, ducts rather short, but slightly bent, apparently exiting to one side of the penisetal follicles. The follicles are separable into *a* and *b* components, and supplied with a moderate amount of copulatory musculature; the setae tubular, tapering gradually, entire; length of mature seta 1.65 mm; midshaft diameter 26  $\mu$ m (mean of 3). Ovaries, consisting of rows of small oocytes in a thin mesentery, together with fairly large, translucent funnels are present in XIII. Spermathecae rather small, equisized pairs, in VIII and IX, each with a simple, sacciform ampulla and sessile diverticular 'collar' occupying the dorsal aspect of the ampulla (ectally), and a short duct arising therefrom. Length of right spermatheca of IX 1.36 mm. Rudimentary development of genital setae in X and XI, with slightly larger follicles in XII (with attachment ligaments). (In P1, the setae of segments X, XI and XII are equally well developed). Setae of XII (H) fairly short, the distal  $\frac{1}{3}$  ornamented with notching that is rather more elongate and densely arrayed than is usual for such setae; length of mature seta 2.26 mm; midshaft diameter 21  $\mu$ m (mean of 3).

### Remarks

*Diploptrema bulburinensis* is distinguished from its congeners in exhibiting metandry, in lacking nephridial tufting, and in the configuration of the genital field (including the three pairs of

'genital seta' swellings in X–XII). It falls within the species-group embracing *D. boardmani*, *D. bifistularis* and ?*D. magna*.

***Diploptrema capella* Blakemore, 1997**

***Diploptrema capella*** Blakemore, 1997: 1795–1797, fig. 3.

**TYPE LOCALITY:** Qld, 23°05'S 148°01'E, Capella, near Emerald, Queensland Department of Primary Industries site, glasshouse soil cores in culture, and on site specimens.

**HOLOTYPE:** RB.94.6.1 (ANIC).

**PARATYPES:** all from ANIC catalogue: RB.94.6.2, P1; RB.94.6.3, P2–P15; RB.94.6.4, P16–18; RB.94.6.5, 9 large specimens and 33 immature; RB.94.6.6 [wrongly recorded as 94.6.5 in ANIC catalogue] P19–P20, and one immature specimen collected from QDPI Capella site.

**Description (after Blakemore 1997)**

Length 50–60 mm. Mass: mean for adults 0.2 gm. Width 2.0–2.5 mm. Segments 96–110; secondary annulation after X–XI (excluding smooth clitellum). Unpigmented; anterior pink with blue tinge; gizzard, hearts, prostates and gut contents visible through cuticle; clitellum beige. Prostomium pro-epilobous to closed epilobous. First dorsal pore 7/8, not obvious, pores continuous on clitellum. Setae 8 per segment from II; *ab* absent from XVIII (replaced by genital marks?); genital setae small on VIII, larger on IX; penial setae large on XVII, smaller on XIX. Setal ratios, mean of three specimens, 6.3:1.0:6.6:0.9:21.7:0.49. Nephropores? Clitellum annular XIII–XVII, ½XVIII ventrally impinged by male field. Male pores minute in XVIII just anterior to setal arc and close to the slightly outwardly bowed seminal grooves between prostatic pores which are equatorial in *ab* line in XVII and XIX; setal papillae raised. Genital markings: genital setae with minute borders on VIII and IX; small paired ventral markings anterior to 16/17, wider and just median to male pores on XVIII, and in 18/19 and 19/20 (this last pair within tumid pad). Female pores in XIV, minute, anterior to *a* setae. Spermathecal pores 2 pairs, on slightly raised papillae in 7/8 and 8/9 in *ab* line.

Septa 5/6 displaced by gizzard, 5/6–9/10 [?] moderately thick, 10/11 and 11/12 close together, from 12/13 thin. Dorsal blood vessel single, continuous on pharynx in IV. Small commissurals in VI–IX, hearts small in X larger in XI–XIII. Gizzard strongly muscular barrel-shaped in V with large anterior flange. Calciferous glands absent. Intestinal origin XV; typhlosole absent but low

thickening of gut on inner dorsal surface from region of XX–XXV. Gut contents fine soil. Nephridia holonephridia commencing from at least VI, avascular, not tufted anteriorly. Holandric, iridescent funnels in X and IX; paired racemose or lobular seminal vesicles posteriorly in IX and anteriorly in XII. Ovaries large but compact palmate, each with 3–4 egg-strings and diaphanous funnels in XIII. Two pairs of tubular convoluted prostates with flaccid ducts in XVII and XIX; glandular parts interlocking. Spermathecae 2 pairs, in VIII and IX; ampulla flattened, tapering to duct with large, flat diverticulum filled with numerous iridescent seminal bodies. Blakemore does not refer to the presence or absence of ventral glands characteristic of the *fragilis* group.

**Remarks**

Blakemore (1997) notes that *D. capella* is similar in some respects to *D. tyagarah*, which itself was believed (Dyne 1979b) to be part of a group that included *D. fragilis*. Especially the distinctive spermathecae, with large diverticula, and the male fields are comparable. He notes that it is separated from *D. tyagarah* by the wider pairing of the spermathecal pores (almost convergent in *D. tyagarah*), differences in the genital markings on XVIII; the additional pair of markings in 19/20 and absence of swelling and genital setae in VII. However, the morphology of *D. tyagarah carnarvoni* significantly lessens the distinction between *D. capella* and *D. tyagarah*, and although *capella* has chronological priority over *carnarvoni*, it is probable that *D. capella* is a junior synonym or a subspecies of *D. tyagarah*.

Blakemore discusses the agronomic potential of this species.

***Diploptrema capricorniae* sp. nov.**

(Figs 26, 27)

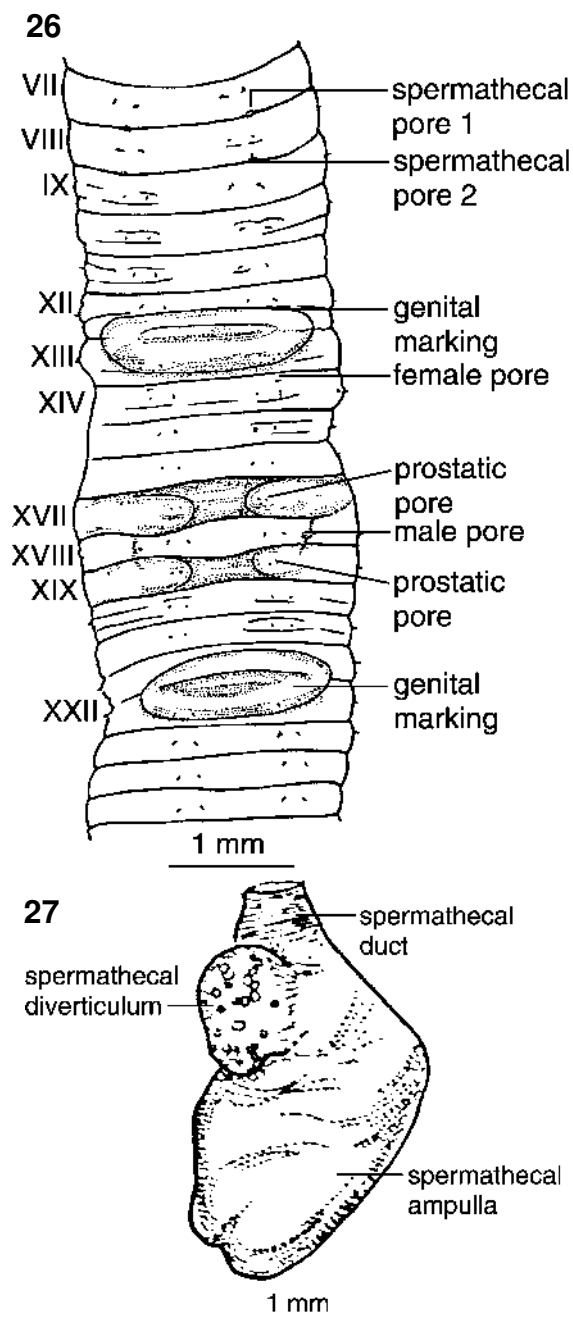
**TYPE LOCALITY:** Qld, 23°22'S 150°32'E, 9.5 km south of Rockhampton, in heavy grey clay under thick grass. Coll. C. Horan, 7 Dec 1969.

**HOLOTYPE:** QMGH 2895.

**PARATYPE:** QMGH 2896.

**Description**

Length 15 (posterior regenerate), 36 mm. Width (midclitellar) 2.0, 1.9 mm; Segments 51, 116 (H, P1). Uniformly circular in cross-section throughout, pigmentless cream-buff in alcohol. Prostomium pro-epilobous, dorsal pores absent. Setae prominent, 8 per segment, in regular longitudinal rows; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; genital setae absent.



**Figs 26, 27, *Diploptrema capricorniae* sp. nov., Holotype.** 26, genital field; 27, right spermatheca of IX.

Nephropores not visible externally. Clitellum apparently annular, developed over XII–XIX, more prominent dorsally, its ventro-lateral limits not

definite in XVII–XIX; setae and intersegmental furrows not obscured. Male pores barely recognisable, as minute points in a post-setal position, immediately adjacent to a pair of extremely faint seminal grooves, in XVIII; the 2 pairs of prostatic porophores, in XVII and XIX, are atop raised mounds, which have their posterior and ventral aspects defined in clear relief by semi-encircling grooves; the intervening region between the porophores is also somewhat depressed. Genital markings two unpaired, median, intersegmental pads of an elongate, ellipsoidal shape and with depressed central regions are present in 12/13 and 22/23 (both markings in H only, 12/13 marking only in P1, P2; remaining specimens immature). Female pores small slits seen presetally, in *bb* lines, in XIV. Spermathecal pores two pairs, in 7/8 and 8/9: simple orifices in *b* lines.

Septa none strongly thickened, but 5/6–10/11 with some muscularisation, remainder diaphanous. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X–XIII the largest of the commissurals, the remainder slight. Supra-oesophageal vessel absent, all hearts dorso-ventral only. Gizzard small, muscularised to some extent, but readily compressed, in V; oesophagus narrow, not highly vascular, and lacking pouching, in VI–XVI; distinction between oesophagus and the narrow intestine indefinite, but probably in XVII; typhlosole absent, but the intestine somewhat thickened. Holonephric; medium-sized funnels ventral of *a* lines, and thin-walled ducts discharging through *c* lines; the nephridial bodies are quite large, in proportion to the body, each occupying a sizeable volume of each segment; pharyngeal tufting absent. Holandric; 2 pairs of (proportionately) very large, convolute, and iridescent sperm funnels in X and XI, with adherent ?spermatic coagulum; testes also visible in XI as conjoined strands adherent to 10/11; 2 pairs of large, robustly loculated seminal vesicles present in IX and XII, of approximately equal size. Prostate glands 2 pairs of tubular, highly coiled organs in XVII and XIX, the anterior pair encroaching on XX, as do the posterior set; both pairs of glands are coiled in 3 planes, giving the appearance of a piled convolution. In all cases, the anterior pair is obviously the larger. Ducts are of short-medium length, straight, and weakly muscularised; a penisal follicle (representing conjoined *a* and *b* components), is associated with each duct; in each case, they contain 4–6 reserve setae, and are ligamented to the mid-dorsal line by a strong, muscular band; the setae long and very thin, irregularly bent, but essentially straight; entire, lacking any ornamentation, the tip apparently flattened and inrolled to form a short tube; length of



mature seta 1.16 mm; midshaft diameter 10  $\mu$ m (mean of 2). Fan-like ovaries, comprising numerous, fused oocytic strings, and large oviducal funnels present in XIII; ovisacs absent. Spermathecae 2 subequal pairs, in VIII and IX, each organ consisting of a large, bulbous ampulla, short duct, and abbreviated, bent diverticulum that appears as an appendage, at the ampulla/duct junction. The ectal end of the diverticular 'arm' contains numerous, iridescent intramural sperm chambers; length of right spermatheca of IX 0.98 mm. Genital setae absent.

#### Remarks

This small species is readily diagnosed by the conformation of the genital field, including the large single tumid pad in 12/13, the absence of genital setae, and the unusual inrolled tip of the penial setae. Its affinities are uncertain.

#### *Diploptrema conwayi* sp. nov.

(Figs 28, 29)

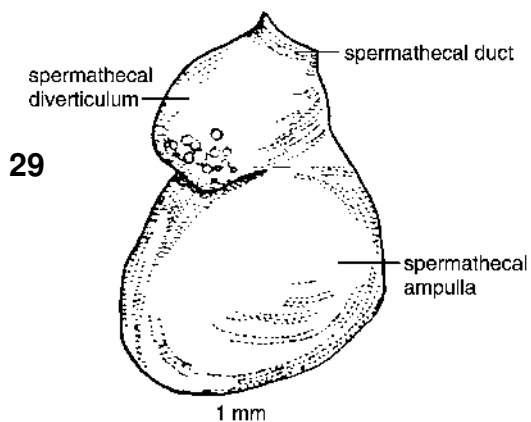
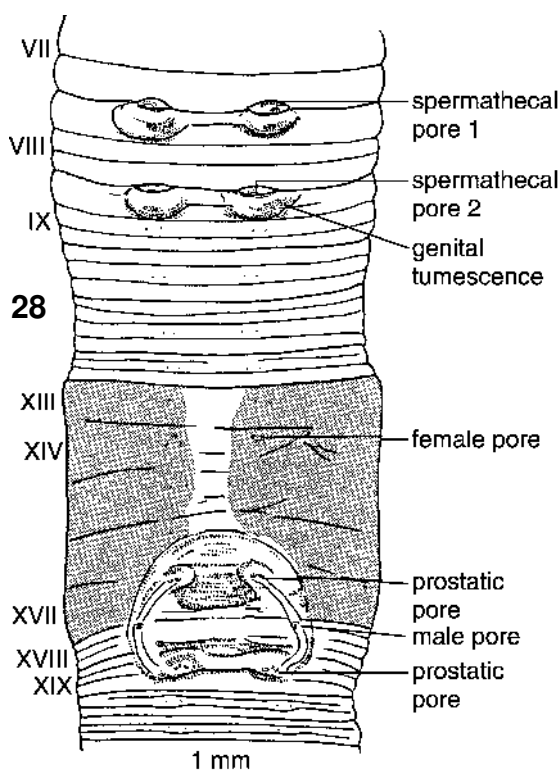
**TYPE LOCALITY:** Qld, 20°21'S 148°46'E, Conway National Park, approximately 300 metres up main walking track, in damp, black, soil and mud, near estuarine swamp. Coll. G. Dyne and A. Postle, 14 June 1974.

**HOLOTYPE:** QMGH 2903.

**PARATYPES:** QMGH 2915.

#### Description

Length 68, 57.5 mm. Width (midclitellar) 6.2, 6.4 mm. Segments 166, 160 (H, P1). Body circular in cross-section throughout, whitish in alcohol, clitellum with slight orange pigmentation. Prostomium prolobous, first dorsal pore in 11/12. Setae 8 per segment, ventral setal couples present on XVIII, those of XVII and XIX modified as enlarged penial setae, those of VIII and IX modified as genital setae. Nephropores occasionally visible on the clitellum; somewhat irregular in position, in the intersegmental furrows:  $\frac{1}{3}$ – $\frac{1}{2}$  distance from *d* lines to the mid-dorsal line. Clitellum strongly developed (more protuberant in P1), saddle-shaped, over XIII–XVII, interrupted ventrally in segments XIII–XV at *b* lines, and even further laterally displaced by the curvature of the male field in XVI and XVII. Male pores fairly conspicuous, lateral of *b* lines, very close to 17/18 (barely within XVIII), in broad, though well-defined, seminal grooves. The latter have incised edges, and join the porophores of a side. The male field is a roughly square, slightly swollen region, with a rounded anterior projection into XVI; within the field are 6 elliptical depressions: the members of the anteriormost pair, in XVII, are inclined at an angle to the X transverse plane, and define the



**Figs 28, 29, *Diploptrema conwayi* sp. nov., Holotype.** 28, genital field; 29, right spermatheca of IX.

posterior boundaries of the raised anterior porophore mounds; the posterior concavities demarcate the raised posterior porophore mounds. Genital markings 2 pairs of tumescences associated with the genital setae lie immediately below the spermathecal pores (all specimens; P1 lacking the posterior right marking); faint glandular strips posteriad of the male field seen in some specimens:

anterior portion of XX in P1, XX, XXI and XXII in P2). Female pores are small slits anterior to *a* setae in XIV. Spermathecal pores on conspicuously protuberant papillae, in 7/8, 8/9 are aligned with *b* setae.

Septa 5/6 diaphanous, 6/7 slightly thickened, 7/8–10/11 moderately muscularised (9/10 the most robust), remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII (only those commissurals in XII and XIII of sufficient size to be termed 'hearts'); these have connectives from both the dorsal vessel and the supra-oesophageal region (a definite supra-oesophageal vessel not demonstrable); remaining commissurals dorsoventral only, extending to VI. Gizzard large and firm, barrel-shaped in V, with thin anterior proventriculus; the gizzard does not encroach on segments beyond VII; oesophagus somewhat truncated, VI–XVI, with 2 pairs of large, vascular outpouchings in XII and XIII (the former pair the larger), with broad, continuous connection to the oesophagus proper. Intestine commences with sudden dilatation in XVII, a dorsal typhlosole present after approx. XXIX, but not developed to any significant degree. Holonephric; nephrostomes large and conspicuous in *ab*, the avesculate ducts opening to the exterior well above *d* lines; pharyngeal nephridia not tufted, but enlarged and convoluted. Holandric; 2 pairs of iridescent spermathecal funnels in X and XI, the anterior pair obviously larger, and associated with flocculent ?sperm masses; 2 pairs compacted seminal vesicles in XI and XII, lying ventro-laterally, beneath the oesophagus. Prostate glands 2 pairs of highly coiled, flattened in tubes in XVII and XIX, both pairs of glands lying parallel to the septation; the anterior pair by far the larger; ducts relatively thin, though fairly long and tortuous. Penisetal follicles closely associated with the prostate glands; these are attached to both protractor ligaments (inserted on the body wall near *b* lines), and retractor muscles (inserted either side of the mid-dorsal line). The setae long and fairly stout, variable in curvature, sometimes sinusoidal; the ectal 1/8–1/10 with irregular clusters of distally directed teeth that are more densely associated near the tip, which is somewhat blunt; the length of a mature seta 4.38 mm; midshaft diameter 49 µm (mean of 4). Small, diaphanous funnels seen in XIII, no ovaries detectable. Spermathecae 2 subequal pairs, in VII and VIII, each consisting of a subspherical ampulla, a short, wide duct demarcated from the latter by a constriction, and a rounded, sessile diverticulum which is little more than a blunt protrusion of the duct wall; the spermathecae discharge posteriorly in their segments, the duct passing through the posterior septa in each

instance. Length of right spermatheca of VIII 2.4 mm; 2 pairs of conspicuous genital seta follicles present in VIII and IX, each flanked by a pair of small, whitish glands which appear to discharge at the ectal end of the follicles as they exit to the exterior; genital setae virtually smooth, with minute, barely perceptible indentations near the ectal end; length of mature seta 1.68 mm; midshaft diameter 35 µm (mean of 3).

### Remarks

Both *Diploptrema conwayi* and the sympatric *D. tenuiseta*, collected from damp soil adjacent to an estuarine inlet, attest to the euryhaline tolerance of at least some members of the genus. The existence of undescribed species of *Diploptrema* on Brampton and Great Keppel Islands is further evidence of the ability to breach narrow marine barriers. Arid terrestrial tracts, on the other hand, appear to present a far more serious impediment to the spread of *Diploptrema* populations. *D. conwayi* is characterised by the presence of the male pores close to 17/18, spermathecae in VII and VIII, and genital seta glands. It is not particularly close (morphologically) to species found in the same region, however.

### *Diploptrema cornutheca* sp. nov.

(Figs 30, 31)

**TYPE LOCALITY:** Qld, 19°54'S 146°35'E, Little Saltwater Creek, 40 km south of Charters Towers. Coll. W. Nash, 5 Jan 1974.

**HOLOTYPE:** QMGH 2932.

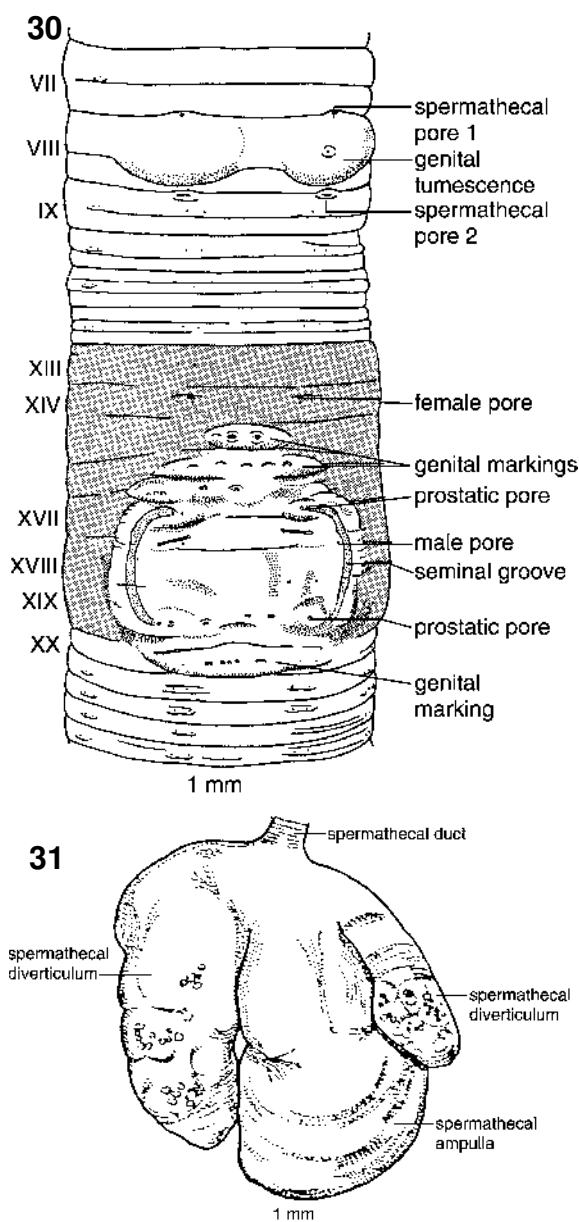
**PARATYPES:** QMGH 2933, 2934.

### Description

Length 96, 84.5 mm. Width (midclitellar) 4.7, 4.6 mm. Segments 200, 224 (H, P1). Body uniformly circular throughout, apparently impregnated with brownish pigment. Prostomium propilobous. First dorsal pore in 12/13. Setae 8 per segment, in regular rows throughout; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; those of VIII replaced by genital setae. Nephropores not visible on the clitellum. Clitellum annular (not encompassing the male field), dorsal pores obscured; extending over XIII–XIX. Male pores indistinct, seen as minute points just ventral of the broad seminal grooves, in the anterior 1/3 of XVIII, slightly lateral of *b* lines. Prostatic porophores on low papillae in XVII and XIX, those of a side linked by the seminal grooves. Genital markings a single, large, dumbbell-shaped swelling in VIII, corresponding to the position of the genital setae (H, P1, P2, P3, P4); a small, median, intrasegmental

swelling with 2 dimple-like markings in XV (H only); a larger (extending across *bb*) marking in XVI (H only) and 16/17 (H, P1, P3), and a similar tumescence in XX (H, P1, P3); within the male field there may be other glandular swellings, the entire field having a slightly convex appearance. Female pores a pair of presetal slits in *a* lines, on XIV. Spermathecal pores 2 well-defined orifices in 7/8, 8/9, in *b* lines.

Septa 5/6–10/11 quite strongly muscularised, 8/9 possibly the strongest; 11/12 moderately thickened, remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those of XI–XIII the largest commissurals, receiving definite connectives from both the dorsal and supra-oesophageal vessels; to the latter vessel is present in IX–XIII. Gizzard medium-sized, firm and barrel-shaped in V; oesophagus moniliform, unelaborated, in VI–XVI; intestine commences with sudden dilatation in XVII, a low dorsal typhlosole commencing in the vicinity of XXV. Holonephric throughout, the stomate bodies giving rise to conspicuous, opaque, avascular ducts that appear to alternate in their entry into the parietes in a regular fashion between mid *bc* and a point far dorsal of *d*, below the mid-dorsal line; a single cluster of tufted tubules present in IV, with composite duct that runs anteriorly, bifurcates, and has at least one branch opening to the exterior at the anteriormost lip of the peristomium. Holandric; 2 pairs of large, convoluted and iridescent spermatic funnels seen in X and XI; 2 pairs of large, finely loculate seminal vesicles present in XI and XIII; vasa deferentia not seen. Prostate glands 2 pairs of tubular organs in XVII and XIX that are much coiled, but compact; the anterior pair, squarish in overall outline, is the larger, and extends posteriorly into XVIII; the ducts fairly long and sinuous, though not thickly muscular. Closely associated with the ducts are penisal follicles of moderate dimensions, each with a strong retractor ligament attached to the body wall just below the mid-dorsal line. The setae quite stout, very gently curving, often with somewhat swollen subterminal portion; the setae have a superficial ribbed appearance due to the presence of numerous apparently regular bracts of flat, jagged teeth that occupy the ectal ½ of the shaft; these teeth appear to be proximally directed, and arranged in broken, circumferential rows. Length of mature seta 1.89 mm; midshaft diameter 55 µm (mean of 3). Long oocytic ribbons and medium-large ovarian funnels are present in XIII. Spermathecae consist of 2 subequal pairs in VIII and IX, each comprising a flask-shaped ampulla, and apparently single diverticulum which is clearly bipartite (contiguous dorsally) and produced as a cornuate outpouching



**Figs 30, 31, *Diploptrema cornutheca* sp. nov.** 30, genital field of Holotype; 31, left spermatheca of IX.

on either side of the ampulla; these excrescences are attached to the dorsal aspect of the ampullal neck, and are continuous with the short, narrow duct. Length of right spermatheca of IX 2.88 mm. Genital seta follicles present VIII, lacking glands; the setae slightly arcing, the distal 3/8 with the usual deep notching; length of mature seta 1.62; midshaft diameter 34 µm (mean of 3).

**Remarks**

*Diploptrema cornutheca* is closely allied to the widespread *D. heteropora*, with which it shares the following characters: alternation of nephropores, tufted nephridia in the pharyngeal region, conservative male field with few genital markings, and absence of *ab* setae on XVIII. *D. cornutheca* may be distinguished from the latter taxon in having only a single pair of genital seta follicles, in the position of the seminal vesicles, and in the different spermathecal construction. In *D. heteropora* the spermathecal diverticulum is single and the spermathecal duct is considerably longer. Duplication of the spermathecal diverticula is an uncommon condition in *Diploptrema*, being seen also in *D. bidiverticulata* and *D. boardmani*.

***Diploptrema crateris* sp. nov.**

(Figs 32, 33)

**TYPE LOCALITY:** (1) Qld, 17°26'S 145°29'E, The Crater (Mt Hypipamee) National Park, simple microphyll vine-fern forest, in granitic soil. Coll. T. Walker, 24 May 1972.

**PARATYPE LOCALITIES:** (1) As above. (2) Qld, 17°34'S 145°36'E, approximately 13 km southwest of Millaa Millaa, on Ravenshoe Road in steep gully in complex notophyll vine-forest. Coll. D. Lambert and G. Dyne, 9 Feb 1975.

**HOLOTYPE:** (1) ANIC GD 95.1.1

**PARATYPES:** (1) 2 ANIC GD 95.1.1; (2) 1 ANIC GD.95.6.1.

**Description**

Length 36+, 95 mm (both posterior amputees). Width (midclitellar) 4.7, 4.5 mm. Segments ? (H, P1). Form circular in cross-section, pigmentless in alcohol, excepting the pinkish clitellum. Prostomium ?prolobous. First dorsal pore 10/11. Setae 8 per segment, commencing on II; ventral setal couples of XVIII present; those of XVII and XIX modified as penial setae; those of XII replaced by genital setae. Nephropores clearly visible on the clitellum, a little irregularly disposed, in the intersegments, at a distance approximately equal to  $\frac{3}{4}bc$  above *d*. Clitellum well developed, saddle-shaped, encompassing segments XIII–XIX, dorsal pores and setae visible. Male pores seen as small slits barely presetal, and slightly lateral of *b*, in XVIII; the pores are located in a pair of narrow, ill-defined seminal grooves that link the porophores of a side. Prostatic pores conspicuous, associated with penial setae, on slightly elevated mounds in XVII and XIX. Genital markings a broad tumescence, extending laterally to *d* lines, and filling segment XII (with slight encroachment into XIII) corresponds to the position of the genital setae, and is present in all

3 specimens available for study; a pair of median, elliptical pads abutting one another in mix-XXV, and occupying segments XXIV–XXVI (H, P1) (P2 macerated in this region). Female pores a pair of orifices atop minute papillae in *ab* (nearer *a*), midway between the setal arc and 13/14, in XIV. Spermathecal pores lie in the intersegments 7/8 and 8/9, in *a* lines.

Septa 5/6, 6/7 moderately thickened, 7/8–9/10 muscularised, but not strongly so; remainder thin. Dorsal blood vessel single; last hearts in XIII; commissurals in XI–XIII conspicuously larger than the remainder, the former receiving connectives from both the dorsal and supra-oesophageal vessels; anterior commissurals dorso-ventral only; supra-oesophageal vessel detected in IX–XIV. Gizzard, large, cylindrical, and highly muscular, in V; by virtue of its length, it dovetails septa posteriorly to 9/10; a thinner (proventricular?) region precedes the gizzard in IV. Oesophagus truncated anteriorly (due to gizzard), remainder with segmental dilatations (?sessile pouches) that are richly vascularised (X–XV); intestine commences with sudden dilatation in XVIII, a low, dorsal typhlosole commencing in XXI; ingesta consists of fine organic particles mixed with soil and mucous strings. Holonephric; stomate nephridial bodies with delicate, avesculate ducts, apparently entering the parietes well above *d*; nephridia in the pharyngeal region enlarged, but not tufted. Incipiently metandric; a large pair of plicate, brightly iridescent spermathecal funnels together with copious seminal coagula seen in XI, and a small pair of transparent funnels (apparently not functional) in X; seminal vesicles demonstrable in XII only (H.) or as a small wisp of loculated material in IX (P1) with much larger masses in XII; the seminal vesicles in XII are attached to the posterior face of 11/12 and surround the oesophagus, the loculi increasing in size ventrally. Prostate glands 2 pairs of coiled, somewhat flattened, tubes; the anterior pair is conspicuously the larger, and directed anteriorly into the preceding segment, whereas the posterior set are restricted to XIX; ducts of medium length (those in XVII with a single bend), moderately muscular. Associated penisetal follicles consist of conjoined *a* and *b* components; copulatory musculature weak. The setae rather short, straight, ornamented on the distal  $\frac{1}{6}$  with short, flattened teeth (singly or in groups) that are sparsely distributed; length of mature seta 1.08 mm; midshaft diameter 21  $\mu$ m (mean of 3). Ovaries, consisting of conjoined oocytic strings, together with large, plicate oviducal funnels, present in XIII; ovisacs absent. Spermathecae 2 subequal pairs in VII and IX, each composed of a tubular,

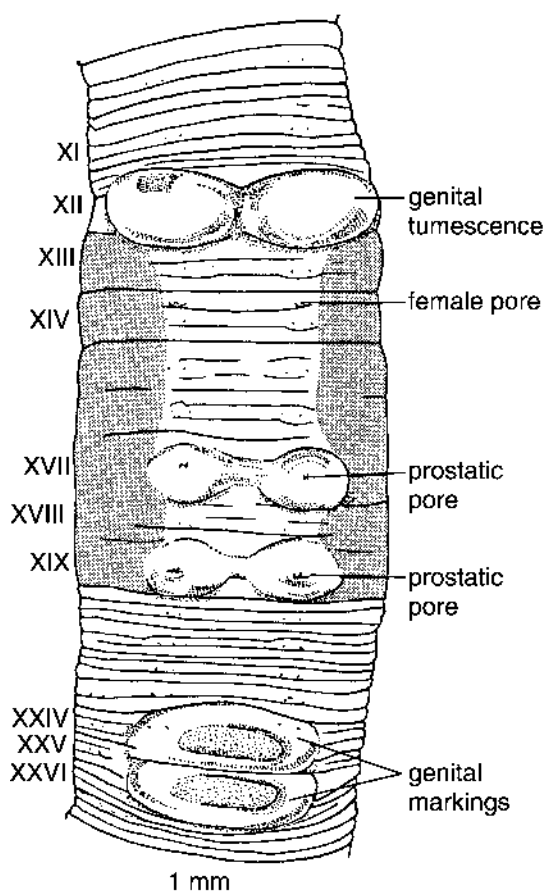


Fig. 32, *Diploptrema crateris* sp. nov., genital field of Holotype.

sac-like ampulla which is dilated ectally into a sessile, horseshoe-shaped diverticular region immediately overlying the pore; duct extremely short, diverticulum copiously inseminated. Length of right spermatheca of IX 1.1 mm. (In P1, the ampulla is more flask-shaped, and in P2, much more elongate). Conspicuous genital seta follicles, with strap-like retractor ligaments, present in XII. The setae very gently curving, unornamented except for some longitudinal striations near the tip, sometimes with a slightly crinkled appearance; length of mature seta 0.96 mm; midshaft diameter 27  $\mu$ m (mean of 3).

#### Remarks

The rudimentary condition of the spermathecal funnels in X and the vestigial nature of the anterior seminal vesicles (if present), indicate that *Diploptrema crateris* is well advanced towards the metandric gonadal condition. The similar state of the male system in two widely separated

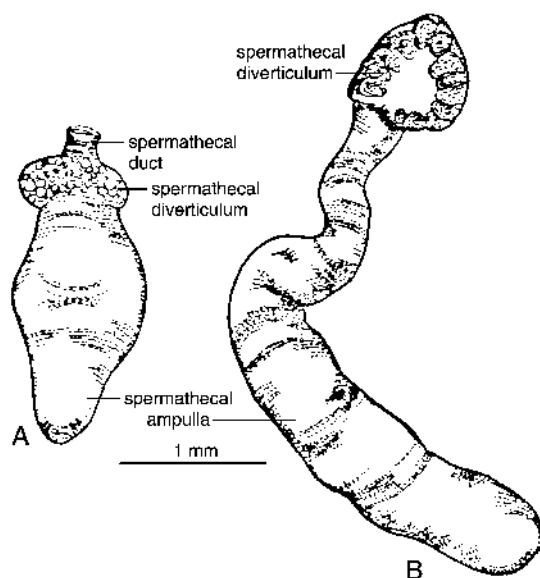


Fig. 33, *Diploptrema crateris* sp. nov.: A, right spermatheca of IX, Paratype 1; B, left spermatheca of IX, Paratype 2.

populations suggests that this phenomenon is not a recent, localised event. Other peculiarities of the species include the unusual position of the genital setae (and their atypical form), and the wide intersetal distance *cd*. *D. crateris* is apparently allied to *D. bidiverticulata*, though differing from the latter in the possession of genital setae, its metandry and in the single, albeit somewhat subdivided spermathecal diverticulum.

#### *Diploptrema daemeli* (Michaelsen 1910)

(Fig. 34)

*Eodrilus dämeli* Michaelsen, 1910: 58–60.

?*Acanthodrilus schmardae* Beddard, 1892: 132.

?*Notiodrilus schmardae*; Michaelsen 1900b: 137 (see *Diploptrema schmardae*, below, which has chronological priority).

*Diploptrema dameli*; Jamieson and Dyne 1976: 450.

**TYPE LOCALITY:** Qld, 23°22'32"S 150°30'49"E, Rockhampton.

**TYPE:** HM V3672 (re-examined). Type USNM #021047. Coll. Damel. Donor, Pickford. Fragments.

#### Description (after Michaelsen 1889; and original)

Length 105 mm. Width 4 mm. Segments? Setae 8 per segment, generally fine and closely paired; ventral setal couples of XVIII absent; those of IX and X enlarged as genital setae; those of XVII and

XIX modified as enlarged penial setae; ventral setal pairs of XI–XVI less closely paired than the remainder (excluding genital setal pairs). Clitellum well developed, saddle-shaped, over XII–XVII, interrupted ventrally between *a* or *b* lines. Male pores equatorial in XVIII, in *b* lines; prostatic pores in XVII and XIX, on rounded papillae, the anterior pair the larger; seminal grooves not clearly demarcated. Genital markings absent. Female pores anteriorly, on XIV, in *ab*. Spermathecal pores on obvious eye-like protuberances; in 7/8, 8/9, shortly median of *c* lines.

Several septa in the male system region thickened. A substantial gizzard present in ?VI, calciferous glands lacking. Nephridia stomate, avascular holonephridia, their slender ducts entering the parietes well lateral of *d* lines. Spermatic funnels 2 pairs, in X and XI; prostate glands tubular, much coiled, in XVII and XIX, the anterior pair the larger. Penial setae enormous, broad and flattened, the ectal ¼ describing an ellipse; ornamentation lacking; penial setae of anterior follicles much larger than those in XVII; length of mature seta (anterior) 3.2 mm, diameter 140 µm; length mature seta (posterior) 2 mm, diameter 120 µm. Genital seta follicles, and large, sacciform internal glands associated with these, are present in IX and X; the setae apparently without distinct ornamentation; length about 1 mm, diameter 50 µm. Spermathecae 2 pairs in VIII and IX, the posterior pair the larger; ampulla sacciform, the duct shorter and a little narrower than the ampulla; a large, multilocular diverticulum fills the dorsal aspect of the duct.

### Remarks

The above description, paraphrasing that of Michaelsen (1910), has been augmented with notes made from a re-examination by Jamieson of the much-dissected type specimen lodged in the Hamburg Museum (V 3679).

Michaelsen (1910) tentatively placed *A. schmardae* in the synonymy of *E. daemeli*, though we should note that *schmardae* has chronological priority. The description of *schmardae* provided by Beddard (1892) was so vague as to allow for agreement on most points, though '*Eodrillus dämeli*' differed in the size of the spermathecal diverticulum, and the form of the penial and genital setae. *Acanthodrillus schmardae* should probably be regarded as a species dubium — its type-material is lost, and the original description is inadequate for diagnosis. *D. daemeli*, on the other hand, is readily distinguished from all other species of *Diploptrema* in lateral displacement of the spermathecal pores to slightly median of *c* lines; the unusually large and flattened penial setae are also of diagnostic value.

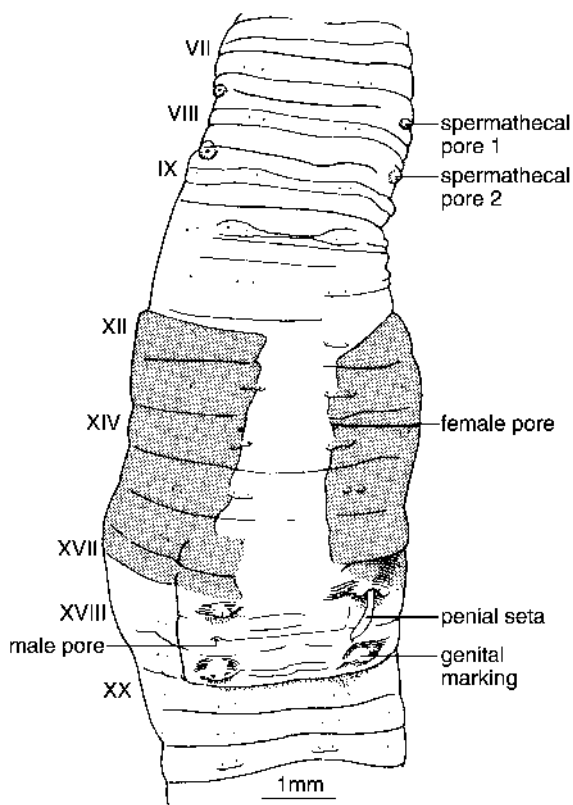


Fig. 34. *Diploptrema daemeli* (Michaelsen, 1910), genital field, of Holotype (?), HM V3679.

### *Diploptrema elstobi* Blakemore, 1997

*Diploptrema elstobi* Blakemore, 1997: 1797–1799, fig. 4.

**TYPE LOCALITY:** Qld, 25°44'S 150°44'E, CSIRO Narayan, near Mundubbera, in brigalow cracking-clay vertisol.

**HOLOTYPE:** ANIC RB.94.7.1.

**PARATYPES:** ANIC RB.94.7.2–4.

### Description (after Blakemore, 1997)

Length (matures) 140–165 mm. Width 2.5 mm. Segments 143–146 (subadults: 132–143; immatures 98–137, mean 120); secondary annulation after clitellum; numerous fine longitudinal lines (blood capillaries?) visible on body wall and lateral yellow spots seen between *b* and *c* on XVII–XVIII in several specimens. Colour in life: body grey with pink anterior and faint blue iridescence; clitellum yellow. Prostomium: propilobous or closed epilobous. First dorsal pore 12/13, indistinct until 18/19. Setae eight per

segment from II, *ab* retained on XVIII, genital setae at VIII and IX, penial setae XVII and XIX. (Setal ratios 6.5: 1.0: 5.8: 0.8: 19.5: 0.47). Nephropores: intersegmental in *c* or *d* lines (slight variation). Clitellum on XIII–XVII just impinging on adjacent segments, annular, excluding the depressed male field. Male pores on XVIII just anterior to *b* setae. Female pores anterior to *a* setae. Genital markings 4 pairs of closely paired ventral pads in 16/17, 17/18, 18/19 and 19/20. Spermathecal pores in 7/8 and 8/9 ventral in *ab* lines.

Septa 4/5 weak; 5/6 and 6/7 medium, adpressed and posteriorly displaced by gizzard; 7/8–10/11 thickened; from 11/12 thin. Dorsal blood vessel single. Hearts XI–XIII; commissurals divide ventrally into numerous capillaries in VI–IX; supra-oesophageal vessels noted in VII–XIV. Gizzard moderately muscular, spherical in V. Calciferous glands absent but oesophagus dilated in VII–XVI. Intestine from XVII; no typhlosole but low dorsal ridge present from about XX. Gut contents: fine soil and organic debris. Nephridia holonephric, sac-like after clitellum; not tufted anteriorly. Male organs holandric, iridescent funnels and adjacent pair of [testes] free in X and XI; compact racemose seminal vesicles in IX and XII. Ovaries: in XIII, as long palmate strands of egg-strings; a small pair of ovisacs in XIV. Two pairs of convoluted tubular prostates in XVII and XIX; ducts short and flaccid overlain by short curved penial setae [form not described]; internal surfaces of male field tumid. Spermathecae two pairs in VIII and IX: ampullae spherical on short ducts each distended dorsally by sessile saccular diverticulum filled with iridescent spermatozoa.

### Remarks

*D. elstobi* superficially resembles *D. capella*, but is larger and has a greater segmental count (Blakemore 1997).

### *Diploptrema eungellae* sp. nov.

(Figs 35, 36)

**TYPE LOCALITY:** (1) Central E Qld, 21°09'S 148°29'E, 3 km from Eungella towards Collinsville, in dense tropical rainforest. Coll. T. Walker, 19 May 1972.

**PARATYPE LOCALITIES:** (1) As above. (2) Qld, 21°08'S 148°30'E, Eagle View Lookout, Eungella National Park, damp, red volcanic soil under rainforest. Coll. G. Dyne and A. Postle, 13 Jun 1974. (3) Qld, 21°11'S 148°32.5'E, Broken River, Eungella National Park, very damp volcanic soil, little leaf litter, under dense rainforest. Coll. A. Postle and G. Dyne, 13 Jun 1974. (4) Qld, 21°07'S 148°31'E, Pease's lookout, 2.5 km from

Eungella, in rainforest. Coll. T. Walker, 18 May 1972. (5) Qld, 21°08'S 148°38'E, Finch-Hatton Gorge. Coll. D. Liem and O. Kelly, 8 Oct 1972.

**HOLOTYPE:** (1) QMGH 2942.

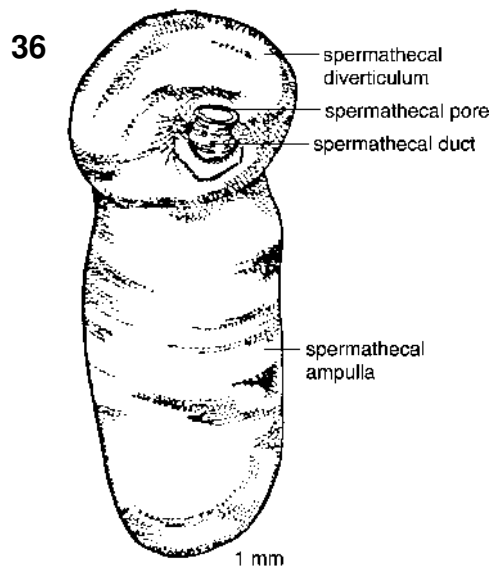
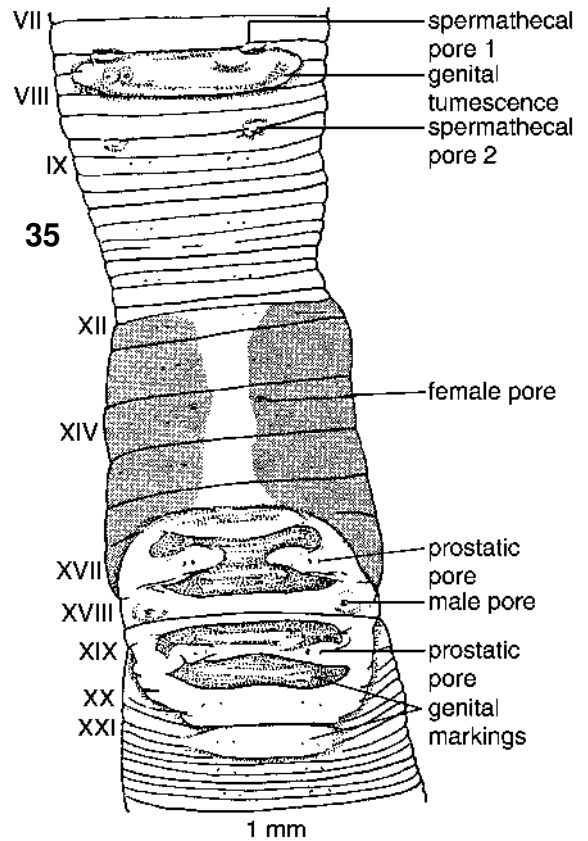
**PARATYPES:** (1) P5, P7–8, QMGH 2945; (2) P2–4, P14, QMGH 2944; (3) P9–12, QMGH 2943; see also 'Palm Circuit', ANIC GD.95.43.7; (4) P13 ANIC GD.95.43.5; (5) P15 ANIC GD.95.55.1.

### Description

Length 156, 129 mm. Width (midclitellar) 4.7, 5.6 mm. Segments 275, 267 (H, P1). Uniformly circular in cross-section, pigmentless buff in alcohol, clitellum a faded pink in some specimens. Prostomium probolous, peristomium extensively furrowed; first dorsal pore in 11/12. Setae 8 per segment, in regular rows throughout, ventral setal couples of XVIII lacking; those of XVII and XIX replaced by grossly enlarged penial setae; those of VIII modified as genital setae. Nephropores not externally recognisable. Clitellum well developed, saddle-shaped over ½XII–XVII, interrupted ventrally in XVII and ½XVI by the male genital field, and anterior of these segments, stopping at *a* lines; intersegmental furrows and setae faintly visible, dorsal pores obscured. Male field consisting of a disc-shaped area with raised margin, enclosing transversely directed ridges and concavities. Male pores seen as conspicuous orifices, situated in mid-XVIII, though displaced laterally, almost in *c* lines (though slightly median of the seminal grooves). Prostatic porophores 2 pairs of raised mounds projecting into the central depressions of XVII and XIX, those of a side conjoined by a narrow seminal groove which follows the contours of the outermost male field rim; the porophores are occasionally armed with projecting penial setae. Genital markings: segment XX with a tumid band continuous with the posterior male field rim (all mature specimens); a glandular pad present in XXI, across *bb* (H, P1) (faintly developed, with intervening depression in 20/21), P2–6, P7 (faint), P8 (as for P1), P9 (as for P1), P10, P11 (faint), P12 (faint), P13 (strongly developed); a single specimen (P4), with a small, median, elliptical marking in 15/16; a faint, glandular patch associated with the anterior projection of the male field into XVI is occasionally present. Female pores a pair of small openings visible presetally slightly lateral of *a* lines. Spermathecal pores 2 obvious pairs with protuberant lips, in 7/8, 8/9.

Septa 5/6, 6/7 slightly thickened, 7/8, 8/9 moderately so, 9/10–11/12 strongly muscularised, 9/10 the most robust, 12/13 thin; septa 10/11 and 11/12 fused so as to encapsulate the organ systems (excl. nephridia) of XI. Dorsal blood vessel single,

continuous onto the pharynx; last hearts in XIII, only commissurals of XII and XIII demonstrably latero-oesophageal (receiving connectives from both the dorsal and supra-oesophageal vessels); the latter vessel seen in X–XIII; remaining commissurals (anterior to VI) diminutive in comparison, and dorsoventral only. Gizzard very large, firm (highly muscularised), an elongate cylindrical organ, in V, but dovetailing septa posteriorly to 9/10, and virtually obliterating the oesophagus in VI–IX; the latter portion of the alimentary canal short, lacking pouching or calciferous glands, in VI–XVI; intestine commences with abrupt expansion in XVII, typhlosole strongly developed. Holonephric; the avesculate ducts of the stomate nephridial bodies enter the parietes well dorsal of *d*, by a distance approximating *bd*; anterior tufting absent, though the nephridia in the pharyngeal region are quite large, and highly coiled. Holandric; 2 pairs of small iridescent funnels with dense sperm masses present in X and XI; 2 pairs of seminal vesicles, moriform, with large loculi, present in XI and XII, the latter pair the larger; vasa deferentia seen as a pair of slightly iridescent tubes coiling on the body wall on each side, the members of a pair apparently fusing only within the parietes. Prostate glands 2 pairs of large, highly coiled tubular organs, with origins in segments XVII and XIX, but extending, in the case of the anterior pair, into XVI and XVIII, with the posterior pair recurved dorsally, over the intestine, and held in place by septum 19/20, through which it protrudes posteriorly; ducts of moderate length, with a simple sinusoidal bend, well muscularised. Penisetae considerable, closely associated with the prostate glands and their ducts, the *a* and *b* follicles closely adpressed in most cases, but separable; the translucent setal bundles are ligamented to near the mid-dorsal line by strong bands of copulatory musculature, the *a* and *b* components with separate, though closely adherent, ligaments; the *a* follicles appear, in general, to be the larger, and contain more reserve setae. The setae strongly curved, in some cases virtually semicircular, occasionally with an additional sinusoidal twist at right angles to the plane of curvature (ectally); the shafts tapering ectally, irregularly clothed with short, narrow spines, length of mature seta 4.97 mm (mean of 3). Ovaries small, with diminutive funnels, in XIII, ovisacs absent. Spermathecae 2 pairs in VIII and IX, the posterior pair the larger; each consisting of a thick-digitiform ampulla, and completely sessile diverticulum which is no more than a bulbous swelling of the ectal end of the ampulla, and which surrounds the spermathecal pore on all sides; duct very short. Length of right spermatheca of IX



**Figs 35, 36, *Diploptrema eungellae* sp. nov., Holotype.**  
35, genital field; 36, left spermatheca of IX.



2.95 mm. A single pair of genital seta follicles present in VIII, associated with 2 pairs of compact glands: a small whitish mass lying close to the nerve cord, and a larger gland located above the follicle; these glands appear to have minute ducts communicating to the exterior along the genital seta follicles; the setae very large, strongly curved, the terminal ectal portion swollen (slightly bulbous); lacking ornamentation of any kind, some fine striae occasionally visible; length of mature seta 2.15 mm; midshaft diameter 58  $\mu$ m (mean of 2).

### Remarks

As noted by Dyne (1984), *Diploptrema eungellae* is probably widespread along the Clarke Range and its spurs, though apparently restricted to rainforest. Its northerly and southerly limits have not yet been determined. Before European settlement, it may have occupied lowland rainforest habitats in the Pioneer Valley, but sampling in this area, now almost entirely given over to sugar-cane production, has yielded no specimens thus far.

*D. eungellae* is readily diagnosed by the very large penial and genital setae (the latter lacking the usual deep notching), a distinctive male genital field, and the presence of seminal vesicles in XI and XII. *D. longiductis*, a coastal species from north of Proserpine, shares many features with *D. eungellae* and appears to be a close relative, though the two taxa are separable on the basis of the more robust body, a much more elongate spermathecal duct, and location of the male pores near 17/18, in *D. longiductis*.

### *Diploptrema falcatooides* sp. nov.

(Figs 37, 38)

**TYPE LOCALITY:** QLD, 22°21.5'S 149°06'E, banks of Lotus Creek, 94 km south of Sarina, in damp black alluvium, ca 0.7 metre above the water table. Coll. G. Dyne and A. Postle, 11 June 1974.

**PARATYPE LOCALITIES:** (1) As above: numerous intact specimens and some fragments (H, P1–6). (2) same locality, coll. C. Horan, 21 Dec. 1969: several intact clitellates, Qld, Lotus Creek, C. Horan, 21 Dec 1969, black muddy soil, several specimens, 2 tagged P13 and P14. (3) Qld, 22°43'S:149°18'E, Stockyard Creek, 145 km south of Sarina, in damp, brown, gravelly alluvium just above the water table, and below it, G. Dyne and A. Postle, 11 May 1974, numerous intact clitellates, immature specimens, and fragments (P8–12).

**HOLOTYPE:** (1) QMGH 2938.

**PARATYPES:** (1) P1–5 QMGH 2939; (2) P13–14 ANIC GD.95.62.1; (3) P8–12 ANIC GD.95.63.1.

### Description

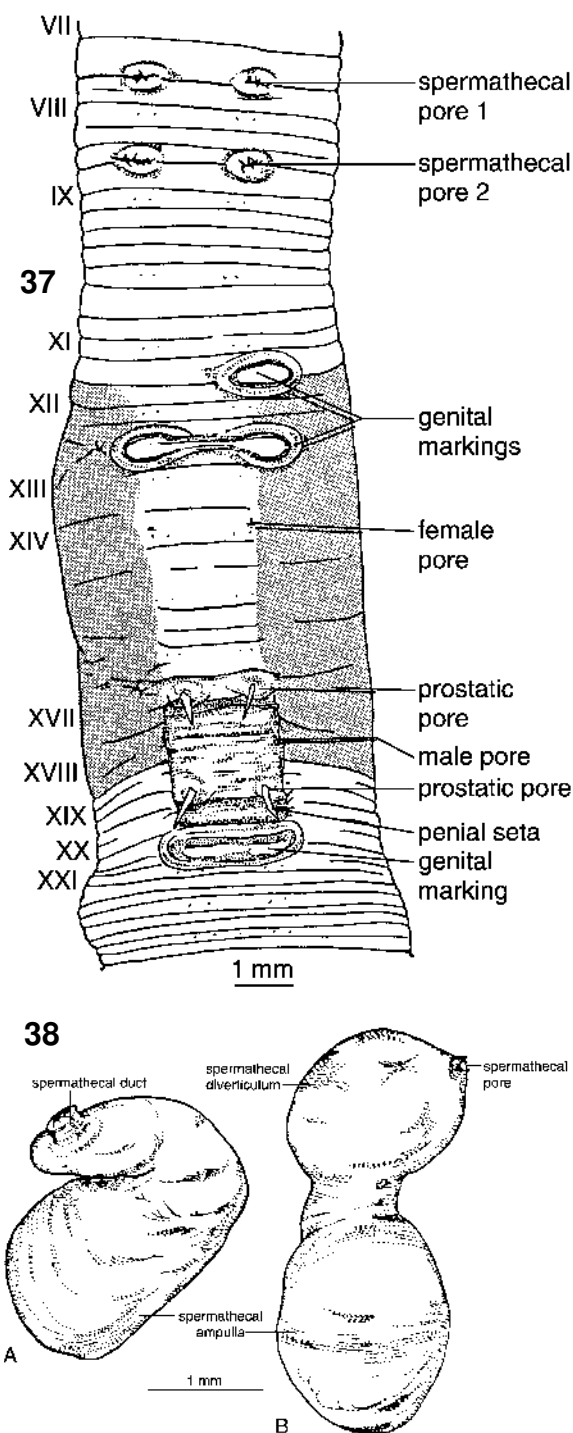
Length 130, 98 mm. Width (midclitellar) 4.8, 5.6 mm. Segments 260, 165 (H, P1). Body uniformly circular in cross-section, pigmentless buff in alcohol. Prostomium tanylobous, peristomium contracted. First dorsal pore in 11/12. Setae 8 per segment, commencing in II, the ventral setal couples of XVIII lacking; those of XVII and XIX replaced by enlarged penial setae; modified genital setae absent. Nephropores often visible on the clitellum, in intersegmental grooves, approximately midway between *d* lines and the mid-dorsal line. Clitellum well developed, saddle-shaped, over XII–XVIII, dorsal pores obliterated, setae and intersegmental furrows obvious. Male pores equatorial, sometimes on distinct papillae, slightly lateral of *b* lines; these lie in narrow seminal grooves that link the prostatic porophores of a side. The male field consists of a deep rectangular concavity, traversed by an alternating series of ridges and depressions, and extending from XVI–mid XX, though the posterior edge is usually extended by a series of transverse depressions centred on the intersegmental furrows; these may fuse broadly to form a continuous concavity, with intermittent tumid bands. The prostatic porophores are deeply fissured, often with protruding penial setae, and are located near the sides of the male field 'trough', in XVII and XIX. Genital markings a pair of eye-like markings extending from *a* lines to mid-*bc*, in each of intersegments 11/12 and 12/13 (in all mature specimens, developed to a greater or less degree); a series of transverse depressions posterior to the male field (see above), centred on the intersegments and often with tumid centres: present in 20/21–22/23 (P4, P9), 20/21–21/22 only (H, P2 (right side only developed in 21/22), P3, P10–11), 20/21 only (P1, P6, P12), rarely, with a single, large transverse marking in 21/22 (P5, P8), and exceptionally, all such markings lacking (P7). Female pores a pair of obvious slits in *b* lines, presetally, in XIV. Spermathecal pores 2 conspicuous pairs on puckered, wrinkled, lips in 7/8 and 8/9, close to *b* lines.

Septa 5/6 slightly thickened, 6/7 moderately so, 7/8–9/10 strongly muscularised, the remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; commissurals in the latter segment and XII only with apparent connections to both dorsal and supra-oesophageal vessels (the latter vessel seen in XI–XIII); remaining commissurals (to VI) still considerable, though dorsoventral-ventral only. Gizzard large, firm and cylindrical, in V, with soft, highly vascular proventriculus; septa to 8/9 directed posteriad due to the gizzard. Oesophagus truncated in the early segments extending from VI–XV,

lacking any conspicuous elaborations; intestine commences in XVI, typhlosole rudimentary. Holonephric; elongate, stomate nephridial bodies give rise to fairly wide ducts that enter the parietes well above *d* lines. Pharyngeal nephridia enlarged but not tufted. Holandric; 2 pairs of small-medium spermatic funnels with coagulated sperm masses present in X and XI; vasa deferentia for the most part, not coiled, fairly straight, and only faintly iridescent; they are free from the body wall until the members of a pair become associated, in XII, and thereafter, remain discrete, fusing only at the male pore; 2 pairs of large seminal vesicle masses present in XI and XII, the constituent loculi rounded and loosely associated. Prostate glands are large, coiled, tubular organs, the anterior pair the larger, with more open coils, adherent to the intestine (not in all specimens) over much of its length, extending posteriorly to XXII (there is some variability as to the shape and extent of these glands); ducts long, sinuous, lightly muscular, entering the parietes in XVII and XIX, near the exit point of the penial setae. The latter are contained in conspicuous translucent follicles, which are ligamented to the body wall by long, strap-like muscle bands that are inserted near the mid-dorsal line, and which pass through the coils of the prostate glands; the setae large, broad and flattened, refracting an orange-red colour, gently curving, though sometimes strongly bent near the tip, which may have a right-angle twist, or a 360° loop; breadth of the shaft remains undiminished to close to the ectal end, though the tip terminated acutely; no ornamentation present. Length of mature seta 2.9 mm; midshaft diameter 44 µm (mean of 3). Genital setae lacking. Ovaries not seen (H) or present as conjoined oocytic strings, in XIII. Spermathecae 2 subequal pairs, in VIII and IX, each consisting of a sacciform or subspherical ampulla connected by a short isthmus (at which the organ is often bent) to a rounded, pulvinate diverticular region surmounting the short duct; in some specimens the diverticulum is narrower hump-like, and the duct longer and more robust. Length of right spermatheca of IX 3.7 mm.

#### Remarks

This species was termed *D. falcata* in manuscript but is named *D. falcatooides* here to avoid potential confusion with *Acanthodrilus falcatus* Beddard, 1897. Lotus and Stockyard Creeks drain into Funnel Creek, itself a tributary of the Isaac River system. One may suppose, therefore, in view of the semi-amphibious habits of this species, and the likelihood of regular fluvial transport for cocoons, that *D. falcatooides* is widely distributed west of the Broadsound Range, perhaps extending further south, into the Fitzroy River Basin.



**Figs 37, 38.** *Diploptrema falcatooides* sp. nov. **37**, genital field of Holotype; **38**, **A**, right spermatheca of Holotype, ventral view; **B**, right spermatheca of Paratype 12, dorsolateral view.

The region between Rockhampton and Sarina, in the rain-shadow of the Broadsound and Connors Ranges, is dominated by brigalow (*Acacia harpophylla*) formations, with occasional sterculiacious vine-thickets; only the latter habitat and the surrounds of perennial streams offer conditions suitable for colonisation by earthworms.

The broad, flattened penial setae exhibited by *D. falcatooides* are reminiscent of those described for *D. daemeli*, as are the spermathecae; the spermathecal pores of the former species, however, are located in the more usual position. The closest congeneric relative of *D. falcatooides* appears to be *D. eungellae*, though the two taxa are readily distinguished on the basis of differences in their genital fields and the absence of genital setae in *D. falcatooides*.

***Diploptrema fragilis* Spencer, 1900**

(Figs 39, 40)

*Diploptrema fragilis* Spencer, 1900: 31–32, pl. IV, figs 4–6.

*Diploptrema fragilis*; Sweet 1900: 114–115, pl. XIV, fig. 6; Michaelsen 1907: 142; Jamieson 1971b: 100–102; Jensz and Smith 1969: 94; Dyne and Jamieson 1998: 488, fig. 1; Blakemore 1997: 1789, 1802.

*Microscolex (Diploptrema) fragilis*; Jamieson and Dyne 1976: 450.

*Plutellus (Diploptrema) fragilis*; Michaelsen 1916: 61.

**TYPE LOCALITY:** Qld, ca 25°37'39"S 151°36'38"E, Gayndah.

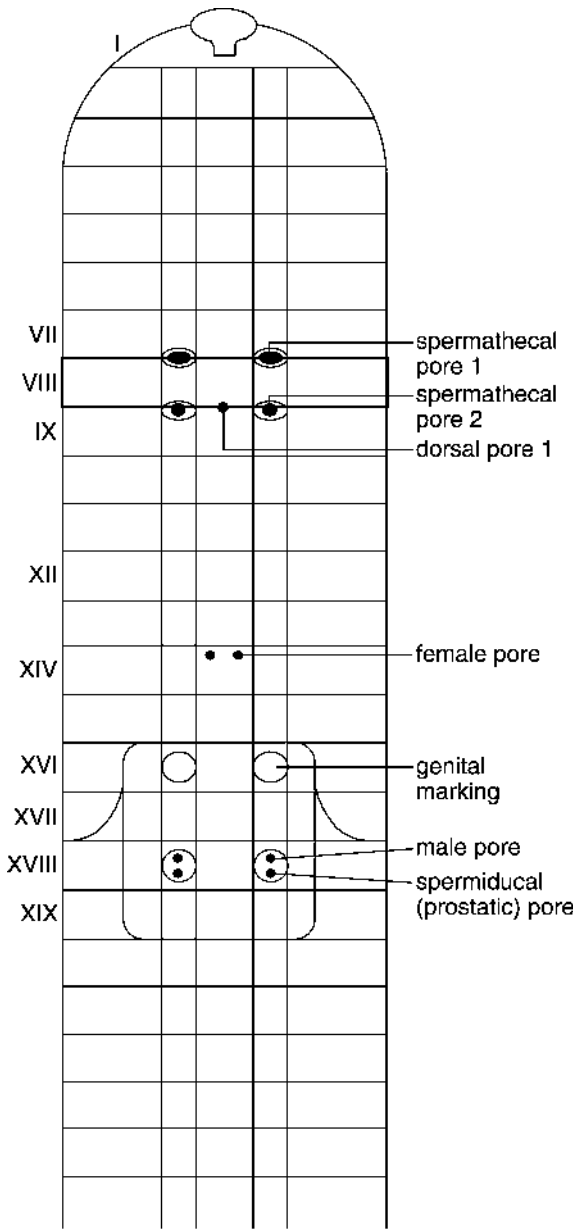
**SYNTYPES:** National Museum of Victoria G31 (many specimens examined; 1 closely); G101, from Cooran not examined.

**Description (after Spencer 1900; Jamieson and Dyne 1976; Dyne and Jamieson 1998)**

Length 25–31 mm. Width 2.0 mm. Segments 111–125. Form cylindrical, anterior end blunt and rounded, slightly bulbous, pigmentless buff in alcohol. Prostomium closed, epilobous 1/2; first dorsal pore (perforate) in 8/9 or 9/10. Setae 8 per segment, closely paired; the ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of VIII and IX as genital setae. Nephropores in *c* lines. Clitellum annular, weaker ventrally, XIII–XVI; dorsal pores obscured, intersegmental furrows and setae only sporadically visible. Male pores minute orifices equatorial, in XVIII. Male field an approximately circular, somewhat tumid area extending longitudinally from the setal arc of XVI to that of XIX, and laterally, in XVIII, beyond *b* lines; small,

indistinct, transversely oval papillae (the prostatic porophores) present in XVII and XIX, at the sites of the modified ventral setal couples. Genital markings: a pair of horny ridges posteriorly in XIV, median to *a* (evidently misidentified by Spencer as the female pores); a median transversely elliptical prominence in 17/18 is possibly a normal feature of the species; segment VIII glandular, and appreciably widened; also (Blakemore 1997) depressed glandular patches extending over XVI–XIX; with ventral pads in 18/19 and 19/20. Female pores minute orifices on a pair of considerable papillae in front of setae *a*, on XIV. Spermathecal pores on a pair of elliptical, slender papillae, in 7/8, 8/9, with centres in *b*.

Septa 5/6 slightly, 6/7 and 7/8 moderately strongly, and 8/9 and 9/10 very strongly thickened, the succeeding three septa slightly thickened, remainder thin. Pharyngeal glands well developed, forming several tiers of flattened, shortly palmate lobes in III, anteriorly. Dorsal blood vessel single, continuous to the posterior portion of the pharynx, flattened and adherent to the intestine in XIV posteriorly; last hearts in XIII, those of X–XIII large, and increasing slightly in size posteriorly; supra-oesophageal vessel present, but its limits not determinable due to maceration. Gizzard large, glossy, but thin-walled, in V. Oesophagus narrow, VI–XIV, calciferous glands or other elaborations absent; intestine commences with abrupt expansion in XV, reaching full width in XVI, a definite typhlosole lacking. Nephridia exclusively holonephric, commencing in II, each invested in a high peritoneum and forming a regular, simple lobe on each side, in each segment; ducts long and avesiculate, entering the parietes in *c* lines. Pharyngeal tufting absent. Holandric; large, thick-walled seminal funnels in X and XI; seminal vesicles 2 pairs of compact, lobulated, and fairly small masses in XI and XII. Prostate glands 2 pairs of flattened, tubular organs, the anterior pair extending to XXII, the posterior set to XXIII; the glands are sinuous, with each bend contiguous with the next; ducts abruptly demarcated, slender, glossy, and running almost straight medially; anterior prostates approximately twice the size of the posterior pair, though the length of the ducts is similar; the ducts enter a median, internal glandular mass extending from XVII to XIX, and corresponding with the external manifestation of the male field. Two penial seta follicles enter the glandular mass in the vicinity of the prostatic ducts, each with a number of setae; the setae slender, narrowly pointed, basally often expanded, gently curved or slightly sinuous, with the ectal ¼ curved through as much as a right angle; the



**Fig. 39.** *Diploptrema fragilis* Spencer, 1900, genital field of Holotype. [Redrawn after Spencer 1900]

ectal end simple, or with a crumpled appearance; minute notching present on the shaft, mostly almost inappreciable. Length of mature seta 1.4 mm (mean of 2); midshaft diameter 40  $\mu$ m. Ovaries moderately stout, long, tongue-like lobes of several large, irregularly arranged oocytes; funnels moderate-sized, simple, also in XIII. A battery of genital setae present in segments VIII

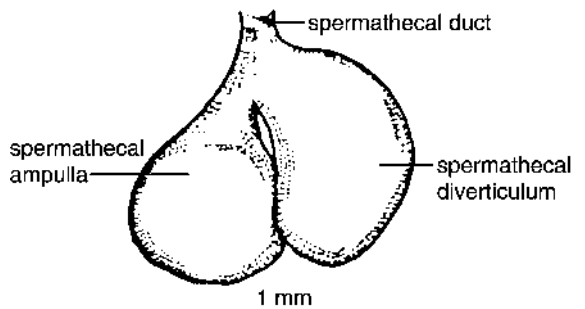
and IX, located behind each spermathecal duct; the setae gently curving, with a broad point, ornamented with the deep, elongate, crescentic notching characteristic of such setae in acanthodrilids, from very near the tip to slightly under halfway down the shaft; length of mature seta 9.98 mm, midshaft diameter 40  $\mu$ m (mean of 2). Spermathecae 2 subequal pairs, in VIII and IX; each with a medially directed ovoid, or spherical ampulla and a lateral, equisized or somewhat longer, iridescent concave-convex diverticulum with intramural loculi. The ampulla and diverticulum share a short narrow duct; length right spermatheca of IX (base of ampulla to pore) = 0.64 mm.

#### Remarks

The status of *Diploptrema fragilis* is discussed in Remarks under the genus.

Dyne and Jamieson attempted unsuccessfully to collect fresh material of *D. fragilis* on several visits to the Gayndah area for this specific purpose, though a further, distinct acanthodrilin *Diploptrema* species was recovered by Dyne from the banks of the Burnett River at Gayndah. Other Spencer species (e.g. *Digaster gayndahensis*) were reportedly collected by Spencer in the 'scrub behind Gayndah'. This site was, prior to felling for pastoral purposes, an extensive area of *Brachychiton*-dominated vine-scrub; if this was the true type-locality for *D. fragilis*, it, like *D. gayndahensis*, may well be extinct.

As noted by Dyne and Jamieson (1998), *D. fragilis* is the nominate 'type' for a species-group that includes three additional known *Diploptrema* species: *D. helonoma*, *D. proserpinensis* and *D. tyagarah*. Members of the *D. fragilis* species-group share the following character set: prostomium epilobous, nephropores in the vicinity of *cd*; slender body form; male pores slightly



**Fig. 40.** *Diploptrema fragilis* Spencer, 1900, right spermatheca of IX, Holotype.

[From Dyne & Jamieson 1998]

presetal; intersegmental markings restricted to the region of XVI–XX; genital seta follicles strongly developed in VII, VIII or IX, often with associated glands; penial setae fine and delicate with little or no ornamentation; pharyngeal tufted nephridia absent; large glandular mass ('ventral glands') located under the nerve cord in XV–XIX; spermathecae divided into a subspherical ampulla and short, blunt digitiform diverticulum bearing numerous sperm chambers on its inner surface (*D. helonoma* diverges somewhat from this latter state). It was noted, however, that most of these unifying characters were symplesiomorphies: only the genital setae glands and ventral glands were considered to represent probable synapomorphies; but genital setae (and their glands) are here considered synapomorphic for a wider acanthodrilid clade. *D. capella*, as it is close to *D. tyagarah carnarvoni*, presumably also belongs to the *fragilis* group though the ornamentation of the penial setae and existence of ventral glands is not mentioned in its type-description.

Unfortunately, the poor condition of the type material does not permit a satisfactory drawing of the male genital field. The uncharacteristically erroneous drawing of Spencer (1900) is reproduced here as Figure 39.

***Diploptrema glareaphila* sp. nov.**

(Figs 41, 42)

**TYPE LOCALITY:** (1) Qld, 19°54'S 146°41'E, 51 km east of Charter's Towers, in gravelly soil. Coll. W. Nash, 5 Jan 1975 (clitellate).

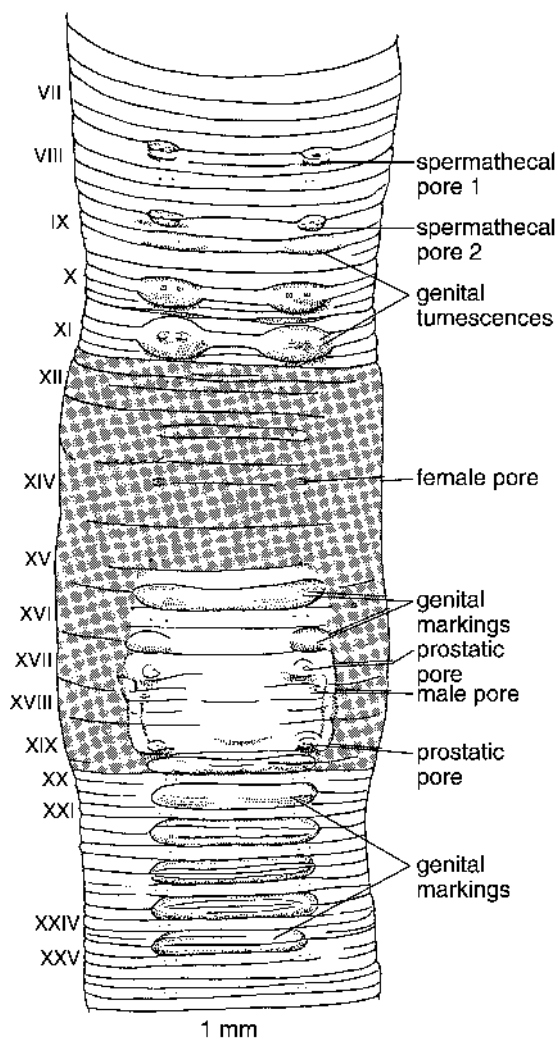
**PARATYPE LOCALITIES:** (1) As above, some juvenile specimens. (2) Qld, 19°54'S 146°35'E, little saltwater creek, 40 km east of Charter's Towers, in moist loam. Coll. W. Nash, 5 Jan 1975: 2 semimature specimens (P1–2), and 4 juveniles.

**HOLOTYPE:** Lodgement unknown.

**PARATYPES:** Lodgement unknown.

**Description**

Length 142, 117 mm. Width (midclitellar) 5.4, 5.9 mm. Segments 279, 262 (H, P1). Body uniformly circular in cross-section, pigmentless buff in alcohol, clitellum darker. Prostomium propilobous; first dorsal pore 10/11. Setae rather small, often difficult to detect, commencing on II, the ventral setal couples of XVII and XIX modified as enlarged penial setae; those of X and XI modified as genital setae; ventral setal couples absent from XVIII. Nephropores clearly visible on the clitellum and in the pre-clitellar region, in *d* lines. Clitellum well developed, annular, though not encompassing the male field, more tumid



**Fig. 41.** *Diploptrema glareaphila* sp. nov., genital field of Holotype.

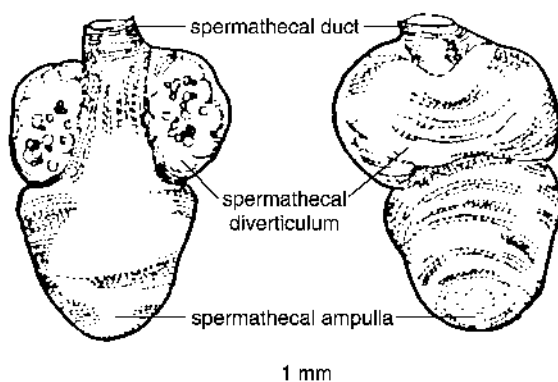
dorsally, over XII–XIX; setae, dorsal pores obscured, intersegmental furrows visible. Male pores seen anterior to the setal arc in XVIII, immediately posterior to intersegment 17/18, and lateral of *b* lines, in shallow seminal grooves. Prostatic porophores small papillae in XVII and XIX. Genital markings 2 prominent, dumbbell-shaped tumescences corresponding to the presence of genital seta follicles in XI and rudimentary ones in X (H, P1–2); a series of regular, raised, intersegmental strips extending across *bb* (or slightly beyond), present in 15/16 (P1 only), 16/17 (midsection not tumid), 19/20–24/25

(H, P1–2). Female pores in *b* lines, presetally, in XIV. Spermathecal pores conspicuous, with elliptical, tumescent surrounds, in 7/8 and 8/9, centred on *b* lines.

Septa 5/6 moderately thickened, 6/7–8/9 very strongly muscularised; 9/10, 10/11 slightly so, remainder diaphanous. Dorsal blood vessel intra-segmentally bifurcate anterior of, and including, XV, conspicuously so in XI–XIII; last hearts in XIII, those of XI–XIII with thin connectives from the dorsal and supra-oesophageal vessels; only the 3 posteriormost commissurals large and heart-like. Gizzard fairly large and muscular, though strongly compressed dorso-ventrally, in V. Oesophagus narrow, moniliform, excepting in segments XII–XIV, where it is dilated and highly vascularised, with a well-developed internal rugosity; intestine commences abruptly in XVIII; a definite dorsal typhlosole present after XXIX. Nephridia commencing in II, the bodies fairly small, and restricted to the region between the ventral and lateral-setal couples; nephrostomes large, prominent, in *ab*; the thin-walled, avesciculate ducts invariably enter the parietes in *d* lines. Tufted nephridia are lacking in the pharyngeal region. Holandric; 2 pairs of iridescent, convoluted spermatic funnels present in X and XI; 3 pairs of acinous seminal vesicles seen in IX, XI–XII, those in XI the smallest. Prostate glands fairly simple, coiled organs, restricted to XVII and XIX, the posterior pair rather smaller, being little more than a simple tube; ducts not highly muscular, straight. Small penisetal follicles are associated with the ducts, copulatory musculature rudimentary; the setae fairly thin, of moderate length, not sharply curving; the upper shaft with a faintly serrated appearance due to very small, widely scattered clusters of ?teeth; length of mature seta 1.87 mm; midshaft diameter 28  $\mu$ m (mean of 2). Ovaries consist of long, membranous ribbons enclosing oocytes of varying size; these and a pair of large, plicate funnels, are present in XIII; ovisacs absent. Spermathecae 2 pairs in VIII and IX, the posterior pair the larger; each consists of a flask-shaped ampulla, the narrow ectal portion of which is all but surrounded by a broad, sessile diverticulum with internal iridescence (when viewed ventrally); the duct is quite short. Length right spermatheca of IX 2.0 mm. Genital seta follicles two pairs, in X and XI, without any associated glands; the setae with regular, longitudinally directed fluting over the distal  $\frac{1}{3}$ ; length of mature seta 0.89 mm; midshaft diameter 30  $\mu$ m (mean of 2).

#### Remarks

As type specimens cannot be located, this species is erected on the illustration and account in Dyne (1984, unpublished) (ICZN 1999: Art. 73.1.4.).



**Fig. 42.** *Diploptrema glareaphila* sp. nov., Holotype, right spermatheca of IX, ventral and dorsal views.

*D. glareaphila* is distinguished from other *Diploptrema* species by the following combination of characters: nephropores in *d* lines, anterior nephridial tufting lacking, dorsal blood vessel bifurcate in the oesophageal region, and two pairs of genital seta follicles, in X and XI. The geographical range of this species is known to overlap that of *D. cornutheca*, but the two species do not appear closely related; the affinities of *D. glareaphila* are uncertain.

#### *Diploptrema helonoma* Dyne and Jamieson, 1998 (Figs 43, 44)

*Diploptrema helonoma* Dyne and Jamieson, 1998: 489–491, fig. 2, 3.

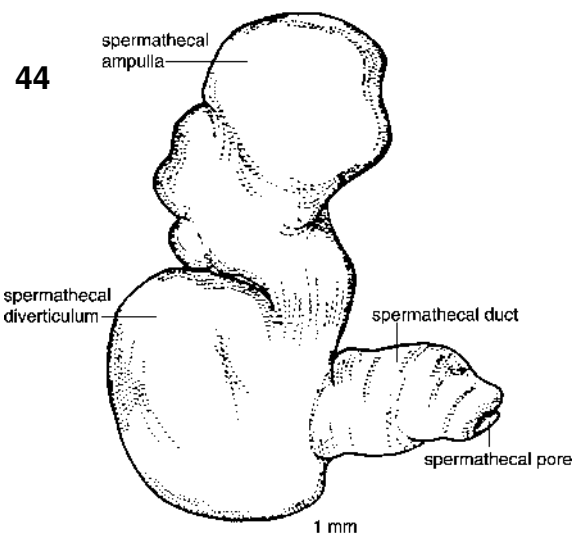
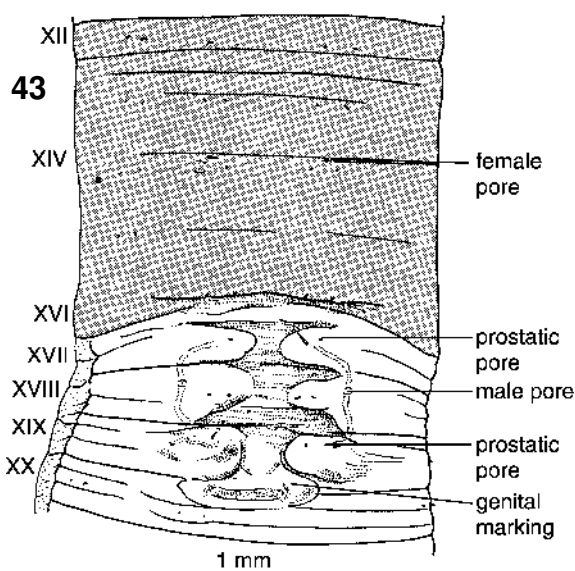
**TYPE LOCALITY:** Qld, 15149'S 2541'E, Ban-Ban Springs, SE Queensland, in black swampy soil at and below the water table.

**HOLOTYPE AND PARATYPES:** ANIC GD.95.144.1; also many specimens not designated types.

#### Description (after Dyne and Jamieson 1998)

Length 113 mm. Width (midclitellar), 2.75 mm. Segments 182. Uniformly circular in cross-section throughout, pigmentless dark buff in alcohol, clitellum with a distinct pinkish tinge, particularly in freshly preserved material. Prostomium epilobous  $\frac{1}{3}$ , closed; first dorsal pore 19/20 (dorsal pores indistinct). Setae 8 per segment, in regular rows throughout; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of VIII and IX replaced by genital setae. Nephropores visible as minute depressions immediately anterior to seta *c* in each segment, by a distance slightly exceeding *cd*. Clitellum annular, obscuring the inter-segmental furrows, though the setae are

prominent; developed over  $\frac{1}{3}$ XII–XVI (better developed dorsally, where it extends to over  $\frac{1}{2}$ XVII). Male pores apparent as 2 obscure orifices at the midpoints of a pair of narrow, ill-defined (shallow) seminal grooves linking the prostatic porophores of a side; the male pores are slightly presetal in position, on XVIII, in *bc*, closer to *b*. Dependent on the state of muscular contraction during fixation, the male field (defined laterally by the seminal grooves, anteriorly by a rhomboidal tumescence, and posteriorly by another genital marking) may be generally concave, which sharpens the relief of the porophores and the ridge joining the male pores, or it may be of a fairly uniform contour. The former condition is presumably assumed during copulation, when the genital orifices would need to be raised for adpression to the partner. The porophores are coincident with the penial seta openings; the setae may be protruded, or withdrawn; each porophore would seem to have only a single seta protruding at any one time. Genital markings a large, unpaired, median rhomboidal (or elliptical) tumescence in 16/17, developed to a greater or less extent in all clitellate specimens examined; a similar marking is present in 19/20; the central confines of the male field (forming 4 depressed areas in contracted specimens) are also glandular, occasionally with pore-like centres. Female pores a pair of pre-setal slits, roughly aligned with *ab*–XVII, calciferous glands or conspicuous outpouchings absent. Intestinal origin in XVII, dilating gradually posteriorly, a definite dorsal typhlosole lacking. Holonephric throughout, the nephrostomes conspicuous on long necks in *ab*; the avesculate ducts open in line with *c* setae, entering the parietes slightly anterior to the setal arc; nephridial bodies are invested in peritoneum, appearing as wafer-like units in each segment. Anterior tufting absent. Holandric; 2 pairs of brightly iridescent spermathecal funnels present in X and XI, and 2 pairs of large, acinous seminal vesicles in IX and XII, the latter pair conspicuously the larger, virtually occupying the ventral portion of that segment. Prostate glands 2 pairs of coiled, tubular organs which encroach on posterior segments to a greater or less degree, penetrating the septa; in all cases, the anterior pair is the larger; prostatic ducts are short, straight and lightly muscular. The entire prostatic region is covered ventrally with a glandular mass which appears to be an internal manifestation of the male field, and which may be responsible for secretions necessary for successful copulation; the prostatic ducts and penisetal follicles pass through this mass prior to entering the parietes. Penisetal follicles (conjoined *a* and *b* components) are equipped with little in the way of copulatory musculature; the



**Figs 43, 44.** *Diploptrema helonoma* Dyne and Jamieson, 1998. **43**, genital field of Holotype. **44**, left spermatheca of IX of Paratype 1. [From Dyne and Jamieson 1998]

setae moderately long, gently curving; the ectal ornamented with irregularly spaced, rounded, deep scallops of variable diameter, with somewhat jagged overhangs; these become more scattered and shallower entally. Length of mature seta 1.90 mm; midshaft diameter 36.2  $\mu$ m (mean of 3). Conspicuous genital seta follicles are associated with each of the spermathecae; the former are surrounded by prominent, discrete, whitish glands,

of which there is one per follicle in IX, and 2 in VIII. These glands are prostate-like, with a definite central lumen, and small ducts discharging to the exterior at the point of emergence of the genital setae; their function is unknown. The setae fairly straight, ornamented over the ectal portion of the shaft (excluding the somewhat swollen apical region) with conspicuous longitudinal fluting; this is due to the alignment of long, longitudinal scallops with fairly smooth edges in this region. Length of mature seta 1.34 mm; midshaft diameter 35.1  $\mu\text{m}$  (mean of 3). Ovaries, consisting of flabelliform clusters of oocytes, and medium-sized ovarian funnels seen in XIII; no ovisacs demonstrable. Spermathecae 2 subequal pairs in VIII and IX, discharging anteriorly in their segments; each consisting of a bipartite ampulla: a clavate or irregular sacciform portion connected by a broad neck to a subspherical part; a small, hemispherical 'diverticulum' is sessile on the ovoid ampullal section, opposite the attachment point of the clavate portion; the medium-sized duct is shared by the two components. The diverticulum is conspicuously iridescent, and contains numerous intramural sperm chambers. Length right spermatheca of IX 1.7 mm (base of ampulla to pore).

### Remarks

*D. helonoma* is the geographically closest species to *D. fragilis*. The similarities in overall morphology between the two taxa leave little doubt as to their phylogenetic propinquity. Points of divergence include the much reduced gizzard in *D. helonoma*, differences in the position of the seminal vesicles and the dorsal pores and the conspicuous development of the genital seta glands in *D. helonoma*.

### *Diploptrema heteropora* (Dyne, 1979)

(Figs 45–48)

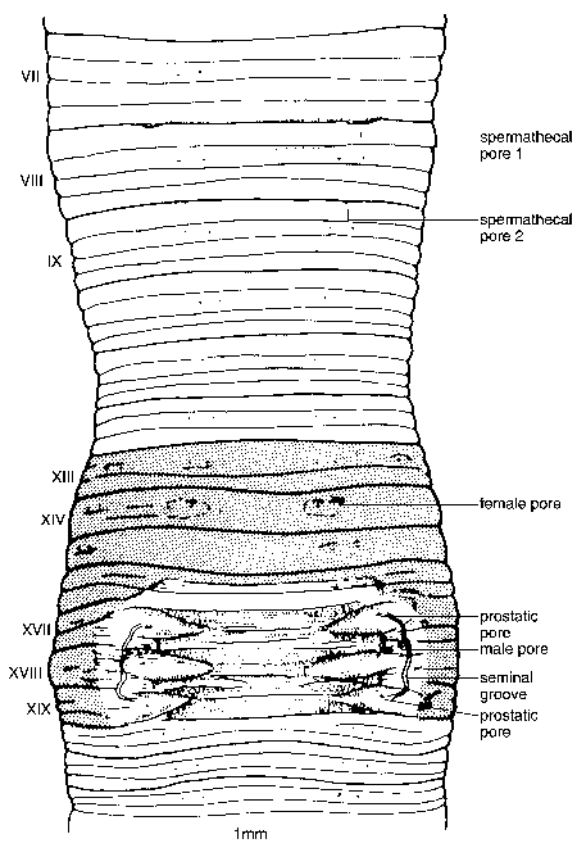
*Microscolex* (*Diploptrema*) *heteropora* Dyne, 1979a: 373–376, fig. 1A–D, table 1, plate 1.

**TYPE LOCALITY:** (1) Qld, 19.30'S 147°02'E, Palm Creek, approx. 33 km S of Townsville.

**PARATYPE LOCALITIES:** (1) As above. (2) Qld, 19°36'S 146°55'E, 7 km E of Woodstock on road to Giru, approx. 40 km S of Townsville. (3) Qld, 19°17'S 146°49', near James Cook University.

**HOLOTYPE:** (1) QM G8890.

**PARATYPES:** (1) QM G8932, AM W6634–5, BM(NH) 1978.1.16; (2) QM G8892–3, AM W6636, BM(NH) 1978.1.17; (3) ANIC GD.95.142.1, QM G8891, 8894–6, AM W6637–6638, GD 1977.1–3, BM(NH) 1978.1.18.

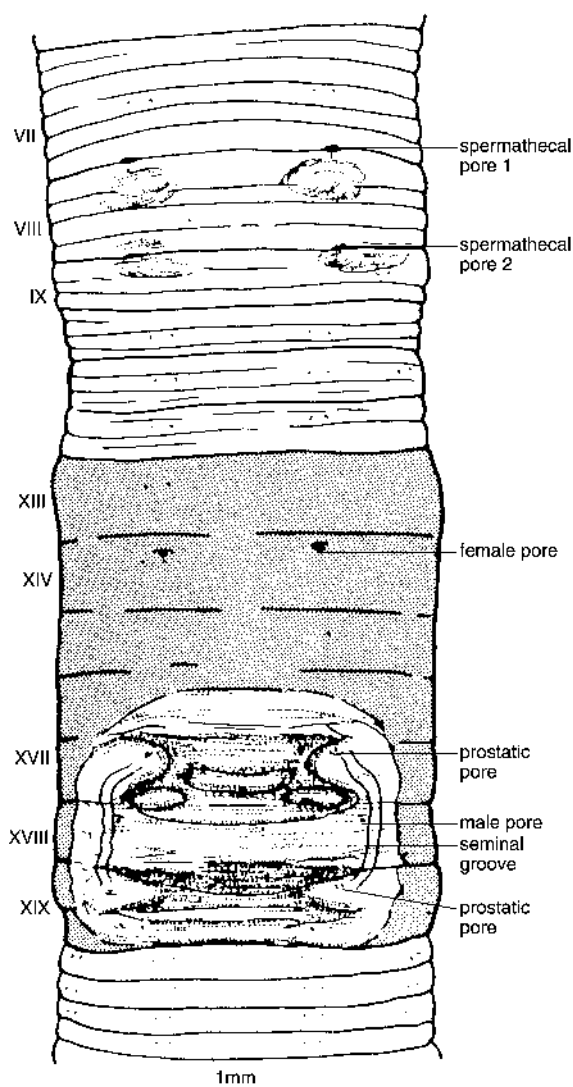


**Fig. 45.** *Diploptrema heteropora* Dyne, 1979, genital field of Holotype. [After Dyne 1979a]

### Description (after Dyne 1979)

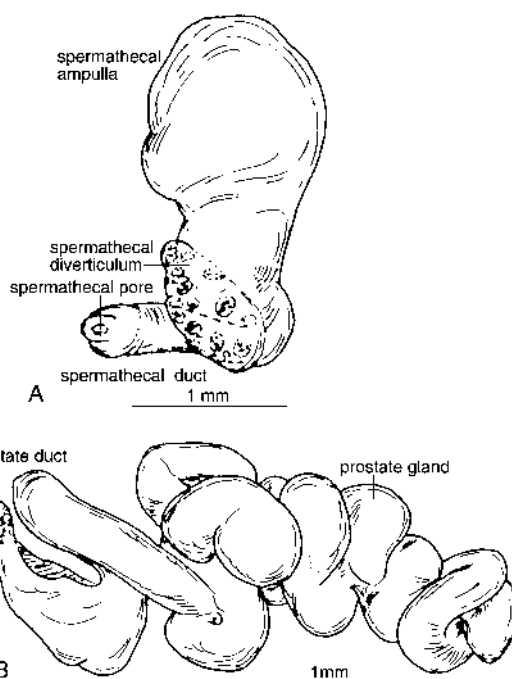
Length 154 mm. Width (midclitellar) = 5.9–7.8 mm. Segments 134–264. Form circular in cross-section throughout; pigmentless buff in alcohol, clitellum purplish-grey. Prostomium probolous, peristomium much furrowed. First dorsal pore 18/19; setae 8 per segment, commencing in II in regularly spaced longitudinal rows throughout; setae *a* and *b* of XVII and XIX modified as penial setae, those of VIII and IX as genital setae, setae *a* and *b* absent from XVIII or in some specimens, rudimentary setae present. Mean setal ratios in localities 1 and 2: *aa: ab: bc: cd: dd: dc: cb: ba* = 11.8: 1.69: 8.86: 1.48: 64.5: 1.43: 8.68: 1.6%; Nephropores visible externally only on the clitellum, alternating between *c* lines (sometimes a little shifted towards *b*) and a position far lateral of *d*, near the middorsal line; the pores discharging in the intersegmental furrows. Clitellum annular, encompassing, with the exception of the male field, segments XIII–XIX, slightly encroaching into XX. Setae and intersegmental furrows only partially obscured on





**Fig. 46.** *Diploptrema heteropora* Dyne, 1979, genital field of Paratype QMG8892. [After Dyne 1979a]

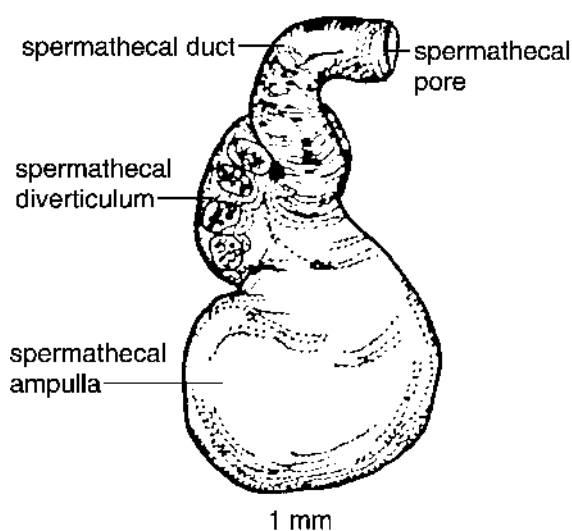
the clitellum. Male pores small points lateral of *b* in XVIII, close to 17/18, located slightly lateral of a pair of well-defined seminal grooves. Prostatic porophores 2 pairs, the trans-segmental pairs conjoined by somewhat sinuous seminal grooves. The central region of the male field (demarcated by the intersegments 17/18, 19/20, and the seminal grooves) is depressed, with the raised porophore mounds projecting ventrally into it; there is a similar ventralwards extension of the male field margin in mid-XVIII. Small interpopulation differences in the configuration of the genital field were observed: one of the specimens from the type



**Fig. 47.** *Diploptrema heteropora* Dyne, 1979, Holotype: **A**, right spermatheca of IX; **B**, right prostate. [After Dyne 1979a]

locality, AM W6634, and particularly some Woodstock paratypes, e.g. QM G8892, possess three additional tumescences within the male field; one elongate marking intermediate between the anterior pair of porophores, the remaining two elliptical, immediately below the porophores; in some specimens, there are additional markings in 19/20 and/or 20/21. Unlike the type, in most specimens, the median ventralwards projections of the male field are produced as to form a single raised median ridge. Considerable variation also exists as to the degree of development of the swelling associated with the genital setae in VIII and IX. Female pores are conspicuous as a pair of small slits (immediately anterior of *a*), in XIV. Spermathecal pores 2 pairs, inconspicuous, situated in 7/8, 8/9, obscured by segmental overlap. A broadly diffuse tumescence associated with the genital setae is discernible in the ventral seta surrounds of segments VIII and IX.

Septa 5/6–9/10 strongly muscularised and thickened, 7/8 the thickest; 10/11 moderately strengthened, 11/12 slightly so. Dorsal blood vessel single; last hearts in XIII. Supra-oesophageal vessel present, traceable only in X–XV or VIII–XIV. Only those commissurals in X–XIII heart-like, with connectives to both the dorsal and supra-oesophageal vessels; the



**Fig. 48.** *Diploptrema heteropora* Dyne, 1979, right spermatheca of IX, Paratype 20.

remainder dorsoventral only, decreasing in size anteriorly. Gizzard large, firm and muscular, in V; oesophagus narrow, internally rugose, lacking pouching or calciferous glands; intestine commences in XIX, XVII or XVIII. Typhlosole developed as a low ridge after XXIX, intestinal walls somewhat thickened in the holotype but not to the same extent in other specimens. Simple stomate holonephridia present throughout, with conspicuous ducts alternating regularly in the position of exit to the exterior; alternation internally appears to be from *cd* to far dorsal of *d*, though the duct apparently travels a short distance within the parietes. Nephridial bladders absent. A large pair of tufted nephridia present in IV, with a well-defined composite duct passing anteriorly. In III, the duct bifurcates, sending one branch dorsally, the other continuing along the ventrolateral body wall; the fate of the two respective ducts was not definitely determinable, though in all probability, they terminate enteronephrically in the buccal cavity. Holandric; 2 pairs of medium-large iridescent sperm funnels present in X and XI, and 2 pairs of racemose seminal vesicles with distinct component loculi in IX and XII. Two pairs of tubular, highly coiled, yet compact, prostate glands in XVII and XIX, each with a muscular, medium length duct passing to the exterior. Vasa deferentia not demonstrable in or obvious as a pair of iridescent tubes winding on the body wall on each side, turning dorsolaterally to skirt the internally glandular manifestation of the male field becoming slightly more swollen, finally entering the parietes, unfused, in XVIII. Two pairs of conjoined (*a* and *b*) penial seta follicles are

associated with the prostatic ducts in XVII and XIX, each containing a number of small, curved, reddish setae, in varying stages of growth; the shaft of mature setae is more or less regularly ornamented with series of very shallow circumferentially orientated indentations; length of mature seta 1.87 mm; midshaft diameter 32.5  $\mu$ m (mean of 2). Two pairs of genital seta follicles are associated with the spermathecal ducts; these follicles are themselves embedded in discrete lobulated glandular tissue. The setae are, but for the proximal and distal extremities, ornamented with a regularly arranged pattern of distally sloping concavities, giving the seta a serrated appearance; the tip is sometimes further elaborated by a pair of longitudinally directed grooves. Length of mature seta 1.02 mm; midshaft diameter 44.2  $\mu$ m (mean of 2). Ovaries, composed of fan-shaped egg-strings, together with plicate funnels in XIII. Spermathecae 2 subequal pairs in VII and IX, each composed of a sacciform ampulla, with sessile diverticulum at the junction of ampulla and duct, the diverticulum internally partitioned into numerous iridescent intramural sperm chambers; the duct long and slightly sinuous; ratio, length spermatheca : length of duct = 3.0.

#### Remarks

Nephropore alternation seen in *D. heteropora* also occurs in *D. cornutheca*. However, the configuration of the genital field is unique and *D. cornutheca* differs in the bipartite spermathecal diverticula. The occurrence of the first dorsal pore in the clitellar region is not elsewhere recorded for *Diploptrema*, though an even further posteriad position is described for *D. eremia* (Spencer 1896), in which the pores commence in the postclitellar region (confirmed in Jamieson and Dyne 1976).

The coelomic fluid of this species is strongly luminescent (Dyne 1979a).

#### *Diploptrema ingrami* sp. nov.

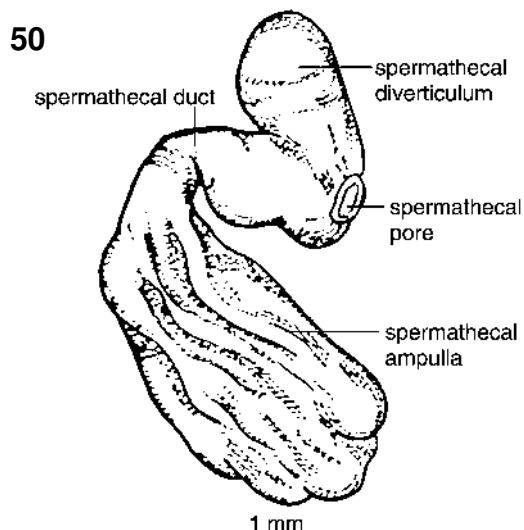
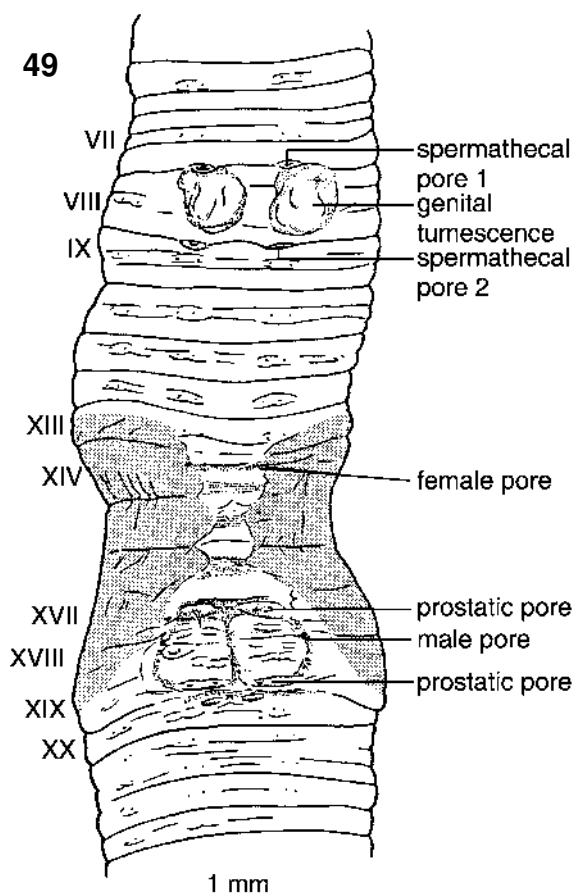
(Figs 49, 50)

**TYPE LOCALITY:** Qld, 12°21'S 141°52'E, Weipa area, along road to Andoom mining site, in open *Eucalyptus* forest, under log in brown-black soil. Coll. G. Ingram, 5 Feb 1975.

**HOLOTYPE:** ANIC GD.95.5.1.

#### Description

Length 83 mm. Width (midclitellar) 5.2 mm. Segments 165 (approximate due to maceration in the mid-body). Body circular in cross-section throughout, buff in alcohol, clitellum a faint pink. Prostomium pro-epilobous, first dorsal pore ?12/13. Setae 8 per segment, commencing in II, prominent due to epidermal shrinkage; the ventral seta couples of XVIII absent; those of XVII and XIX



Figs 49, 50, *Diploptrema ingrami* sp. nov., Holotype. 49, genital field; 50, right spermatheca of IX.

modified as penial setae, those of VIII replaced by genital setae. Nephropores not externally recognisable. Clitellum tumid, some-what wrinkled, saddle-shaped, in  $\frac{1}{2}$ XIII– $\frac{1}{3}$ XIX, with a mid-ventral gap of varying width, dorsal pores obscured, setae and intersegmental furrows usually visible. Male pores seen as small slits, just below 17/18, and lateral *b* lines, in narrow, though well-defined seminal grooves; the latter join the prostatic pores of a side in a semicircular arc. Prostatic pores, coinciding with the ventral setal couples of XVII and XIX, not significantly elevated; the male field roughly circular, containing some slight convexities with irregular glandular patches. Genital markings a single pair of subcircular swellings corresponding to the genital seta follicles, in VIII, located between the 2 pairs of spermathecal pores, no other genital markings (apart from those contained within the male field) visible. Female pores small orifices seen presetally, in *a* lines, difficult to discern due to deep intrasegmental furrowing in the clitellar region. Spermathecal pores 2 pairs, in 7/8 and 8/9, aligned with mid *ab*.

Septa 6/7 slightly thickened, 7/8–8/9 moderately muscularised, 9/10 and 10/11 strongly so, 11/12 moderate, remainder diaphanous. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, commissurals in X–XIII conspicuously larger than the more anterior vessels, and apparently receiving connectives from both the dorsal vessel and the vascularised dorsal aspect of the oesophagus (a definite supra-oesophageal vessel lacking). Gizzard large, strong, with muscular sheen in ?VI (septum 5/6 not seen); oesophagus narrow, the transition between it and the intestine gradual; (the oesophagus dilating over segments XIV–XIX) calciferous glands and/or pouching lacking. A very prominent bipartite dorsal typhlosole commences abruptly in XXIV. Nephridia stomate holonephridia throughout, with the exception of the bodies in IV, which are elaborated as tufted nephridia, the wide, composite ducts of which were traced anteriorly to the buccal cavity; nephridia in V–VII also highly coiled and enlarged, but not tufted. Midbody nephridia comparatively simple, elongate tubes with avascular ducts alternating regularly in their position of exit to the exterior, from mid-*bc* to a point above *d* approximately equal to the distance  $\frac{1}{2}$  *bc*. Holandric; 2 pairs of medium-sized iridescent funnels and associated sperm masses seen in X and XI; 2 pairs of racemose seminal vesicles with a stranded appearance present in IX and XII; vasa deferentia not seen. Prostate glands 2 pairs of lobed and incised tubulo-racemose organs in XVII and XIX, the anterior pair the

larger, and bent into an S-shape; the ducts short, and like the penisetal follicles, enter the body wall through a glandular mass lying beneath the nerve-cord in XVII–XIX. Penisetal follicles fairly large, with numerous reserve setae and extensive copulatory musculature; the setae fairly broad, narrowing ectally, unornamented except for the closely arranged circumferential striations that cover the entire shaft; length of mature seta 2.24 mm (mean of 3). Ovaries, comprising small oocytic sheaves, and small, diaphanous funnels seen in XIII. Spermathecae 2 pairs, in VIII and IX, each consisting of a somewhat shrivelled sacciform ampulla with a narrowed neck portion that shares the very short duct with a blunt, rounded diverticulum that is rather short; the ampullae usually penetrate anteriorly through the septa to lie in the preceding segments. Length right spermatheca of IX = 3.6 mm. Genital seta follicles a single pair, in VIII, under the spermathecae in that segment; the setae fairly straight, the ectal region somewhat swollen, but with acutely pointed tip, giving a hastiform appearance; the upper ½ of the shaft ornamented with narrow, fairly widely spaced indentations giving a serrated appearance, though these are lacking from the swollen ectal portion. Length of mature seta 1.64 mm; midshaft diameter 40 µm (mean of 3).

### Remarks

The tubulo-racemose nature of the prostate glands in *Diploptrema ingrami* has also been suggested by histological sectioning. This feature, together with the conspicuous typhlosole (both features, however, seen in *D. scheltingai*) and alternating nephropore arrangement would appear sufficient to delineate the species, although examination of a much larger series of specimens will be necessary to confirm these anatomical attributes. The position of the gizzard (in VI) also requires verification. The species is apparently unrelated to *D. heteropora*, nephropore alternation notwithstanding, and has independently acquired this nephridial modification.

### *Diploptrema inornata* sp. nov.

(Figs 51, 52)

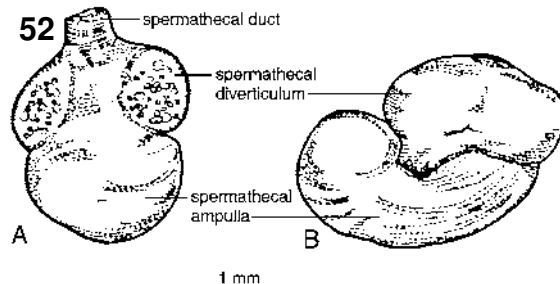
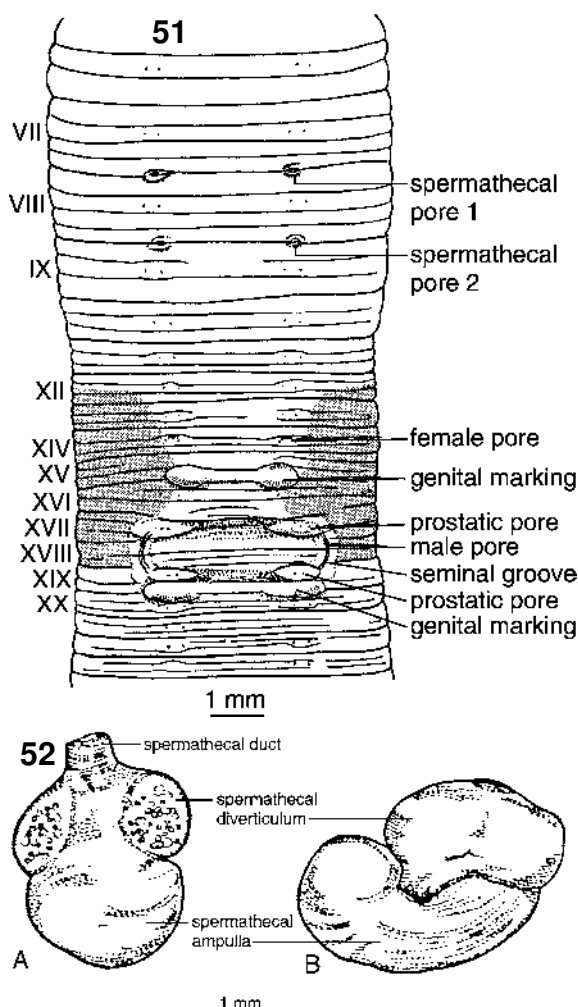
**TYPE LOCALITY:** Qld, 20°00'S 148°05'E, Spring Creek, approximately 16 km west of Bowen, on the Bruce Highway, in sandy soil in creek bed near bridge. Coll. G. Dyne and D. Lambert, 4 Feb 1975.

**HOLOTYPE:** QMGH 2922.

**PARATYPE:** QMGH 2923.

### Description

Length 105, 97.5 mm. Width = 6.1, 6.0 mm. Segments 269, 274 (H, P1). Body uniformly circular in cross-section throughout, pigmentless



**Figs 51, 52, *Diploptrema inornata* sp. nov., Holotype.** 51, genital field; 52, A, right spermatheca of VIII, ventral, B, right spermatheca of IX, dorsal.

buff in alcohol, clitellum brownish. Prostomium prolobous; first dorsal pore 11/12. Setae 8 per segment in regular longitudinal rows throughout; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae, genital setae lacking. Nephropores sporadically visible on the clitellum as irregularly disposed points, in some segments apparently alternating from between slightly below *c* to a point above *d*. Clitellum saddle-shaped, not developed to tumescence, more conspicuously developed dorsally, over ½XII–XVIII; dorsal pores, inter-segmental furrows and setae not obvious. Male pores seen in XVIII, immediately posteriad of 17/18, in the shallow seminal grooves that join the prostatic porophores of a side. The latter are

not prominently developed, and lie in transverse furrows that run across XVII and XIX. Genital markings a pair of small, rounded swellings immediately posteriad of the porophores in XIX (in 19/20) (H, P1–2); a similar though larger, pair anterior to the porophores in XVII, centred on *a* lines, in 15/16 (H, P1 (right side only, P2); a further, less well developed pair seen in P1 and P2 immediately anterior to the porophores in XVII. Female pores immediately anterior to the setal arc, in XIV, in *ab* (closer to *a*). Spermathecal pores 2 inconspicuous openings centred on *ab*, in 7/8 and 8/9.

Septa 5/6 moderately muscularised; 6/7–10/11 strongly thickened with muscular tissue (7/8–9/10 the thickest). Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII, both these and the commissurals in XII the only contractile vessels large enough to be considered hearts, though those in X and XI, like the latter, are latero-oesophageal; remainder decreasing in size antieriad, and dorsoventral only. Gizzard large and muscular, in V, with soft anterior proventriculus that is reflexed over the early part of the gizzard; oesophagus rather short and narrow, lacking any elaborations, in VI–XV; intestine begins with sudden dilatation in XVI, a typhlosole apparently lacking. Holonephric; stomate, avesculate nephridial bodies throughout (anterior tufting in the pharyngeal region lacking); fate of ducts indefinite due to poor preservation, but some irregularity of nephropore position, centred on *cd* noted externally. Holandric; 2 pairs of well-developed spermathecal funnels and associated coagula present in X and XI; 2 pairs of finely loculate seminal vesicles seen in IX and XII. Prostate glands 2 pairs of simple tubular organs restricted to their segments of origin (XVII and XIX), the anterior pair clearly the larger and more functional pair; ducts very short and straight, not highly muscular, opening confluent with the penisetal follicles. The latter well developed, each with numerous setae and endowed with strong copulatory musculature linking it to the body wall. The setae gently arcing, the ectal end often with a more acute bend; the ectal 1/8 of the shaft with a serrated appearance due to the presence of regular, ?incomplete circumferential bands of distally directed jagged toothlets; the tip invariably blunt. Length of mature seta 2.20 mm; midshaft diameter 56.9  $\mu\text{m}$  (mean of 3). Diaphanous oocytic membranes bearing series of very small oocytes, and small funnels present in XIII. Spermathecae 2 subequal pairs in VIII and IX, each consisting of a tubulo-sacciform ampulla, the dorsal aspect of which is surrounded at its ectal end by an irregular, sessile diverticulum that forms a partial 'collar';

the ampulla and the diverticulum share a short duct; diverticulum containing numerous intramural sperm chambers with obvious iridescence. Length left spermatheca of IX = 1.9 mm. Genital setae absent.

### Remarks

*Diplotrema inornata* may be distinguished by the combination of a lack of genital setae, and the location of the male pores close to 17/18, with the seminal vesicles situated in IX and XII. It may be grouped with a number of species from the central Queensland region, all of which exhibit the shifting of the male pores far antieriad in XVIII. This species-group includes: *D. conwayi*, *D. spectabilis*, *D. sulcata* and *D. tenuiseta*. Sampling from this region, and the important Burdekin River catchment area has, unfortunately, been very superficial. Considerably more investigative work would need to be carried out before an accurate picture of diversity and spatial/morphological relationships can emerge. The lack of genital setae exhibited by *D. inornata* (as in *D. armatissima*, *D. intermedia* and *D. minuta*) emphasises what little importance can now be placed on this character at the generic level, though presence of these setae characterises a wider acanthodrilid clade.

### *Diplotrema lamberti* sp. nov. (Figs 53, 54)

**TYPE LOCALITY:** Qld, 22°35'S 149°14'E, Spring Creek, approximately 116 road km north of Marlborough (Queensland Museum catalogue states 'circa 183km N of Rockhampton'), under bridge in creek bank in black, muddy alluvium. Coll. G. Dyne and D. Lambert, 5 Feb 1975.

**HOLOTYPE:** QMGH 2916.

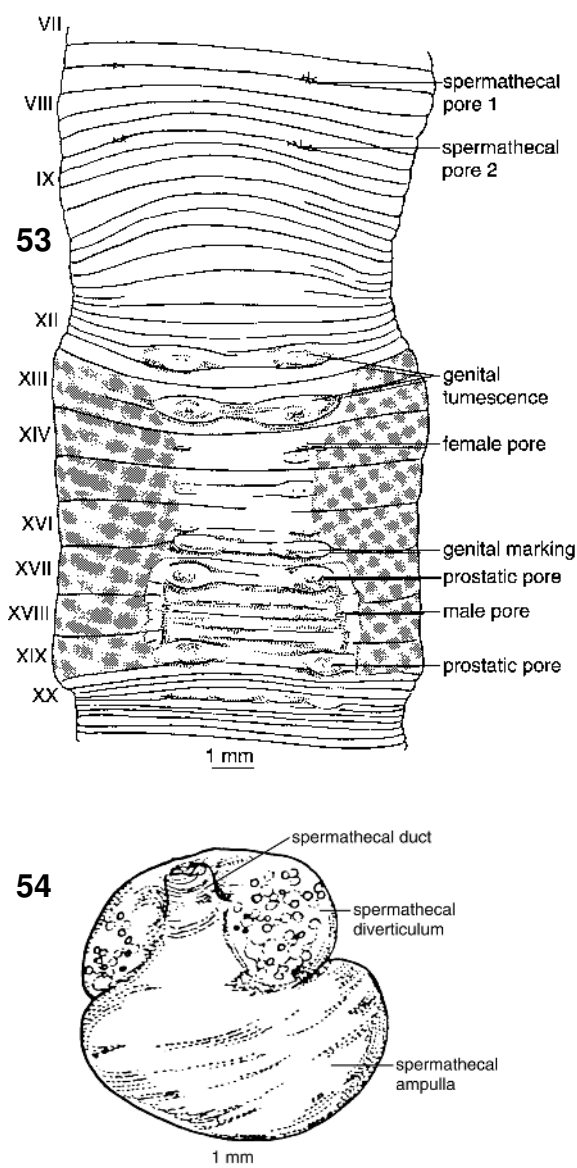
**PARATYPES:** QMGH 2917; ANIC GD 95.64.1.

### Description

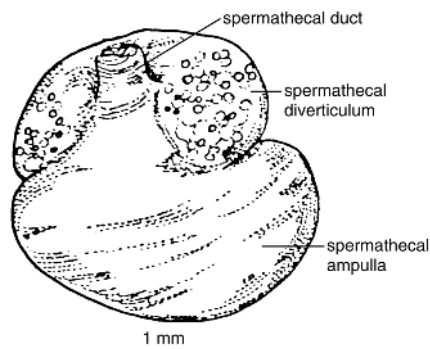
Length 128+, 85 mm. Width (midclitellar) 9.1, 8.0 mm. Segments ?, 195 (H-posterior amputee, P1). Form circular in cross-section throughout, pale cream in alcohol, clitellum pinkish. Prostomium probolous, first dorsal pore 11/12. Setae 8 per segment, commencing in II; dorsal setal couples usually indistinct; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; those of XII and XIII replaced by genital setae. Nephropores obvious as a straight line of small orifices on the clitellum, intersegmentally, in *cd*. Clitellum well developed, saddle-shaped, over XIII–XX; the setae and dorsal pores obscured, intersegmental furrows visible. Male pores a pair of small orifices in fairly straight, shallow, seminal grooves; the pores are above the setal arc, lateral of *b* lines. Prostatic

pores 2 pairs, apparently opening via the penial seta orifices, in XVII and XIX, surmounting porophore mounds that form the corners of a rectangular male field; a raised strip adjacent to the seminal grooves defines the field laterally, and the slightly tumid bands joining the porophore mounds of a segment define the anterior and posterior boundaries. Genital markings pre- and post-clitellar accessory markings absent; narrow dumbbell-shaped markings associated with the genital seta pores present on XII and XIII (in all specimens examined); the holotype bears a pair of small swellings immediately anterior to the porophores in XVII. Female pores small slits on small papillae, approximately aligned with *b* lines; spermathecal pores 2 pairs, in 7/8 and 8/9, difficult to discern due to their insunken position, in *b* lines.

Septa 5/6 thickened, 6/7–9/10 similarly muscularised (9/10 the strongest), septum 10/11 partially aborted, attached dorsally and laterally to the anterior face of 11/12, rather than the body wall, and effectively encapsulating the alimentary and major vascular components of that segment in a purse-like structure; 12/13 slightly thickened, the remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, the only other commissurals of comparable size being in XII; those of XI rather diminutive in comparison to the latter; commissurals of XII and XIII are the only ones in which connectives from both the dorsal and supra-oesophageal vessels are clearly demonstrable. Gizzard large, firm and dolioform, in V, with a definite, soft, cap-like proventriculus; septa posteriad to 8/9 dovetailed due to gizzard size; oesophagus rather short, vascular internally rugose, in VI–XVI, lacking any dilatations or calciferous glands. Intestine commences with an abrupt expansion in XVII, a low, dorsal typhlosole (little more than a simple fold) is present after approximately XXVI. Excretory system holonephric; a single pair of stomate, exonephric nephridial bodies per segment, commencing in II, their avesciculate ducts discharging in *cd*; anterior tufting absent. Metandric; a single pair of small, non-iridescent spermatid funnels present in XI only, where they are effectively encapsulated due to the unusual septation described above; a pair of finely loculated seminal vesicles present in XII. Prostate glands 2 pairs of tightly coiled, tubular organs restricted to XVII and XIX, the former pair the larger; prostatic duct quite short, poorly muscularised. Penisetal follicles present, and closely associated with these ducts, copulatory musculature not extensive. The setae curved in a gentle arc, the upper 1/8 with fairly regular, though sparse, bands of very short serrations, extreme



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**Figs 53, 54, *Diploptrema lamberti* sp. nov., Holotype.**  
53, genital field; 54, right spermatheca of IX.

ectal region entire; length of mature seta 1.52 mm; midshaft diameter 37.7  $\mu$ m (mean of 2). Ovaries seen as a small tuft of immature oocytes, together with diaphanous ovarian funnels, in XIII. Spermathecae 2 pairs, in VIII and IX, the posterior pair the larger; each organ consisting of a subspherical ampulla, separated by a broad constriction from a diverticular sac that all but envelops the short duct. Length right spermatheca

of IX = 2.1 mm. Genital seta follicles well developed, in XII and XIII, the setae entering the parietes through the centre of a torose annulus, and exiting to the exterior through discrete slit-like pores; the follicles are provided with obviously functional bands of retractor muscles inserted in the lateral body wall musculature. The setae gently curving, only the ectal 1/5 with conspicuous narrow notching characteristic of the genus; length of mature seta 1.29 mm; midshaft diameter 35  $\mu$ m (mean of 3).

### Remarks

The possession of genital setae in the region XII–XIII is peculiar to *D. lamberti*. Whether this species deserves inclusion in the *D. boardmani* species-group (two members of which have genital seta follicles in X–XII, the condition nearest that seen in *D. lamberti*) is conjectural; the structure of the spermathecae and details of the nephridial system are not inconsistent with such a placement, and the metandric condition of the gonads is reminiscent of *D. bulburinensis* and *D. jamiesoni* (a dubious member of the above grouping). Conversely, there is a sharp discontinuity between the morphological organisation of *D. lamberti* and that exhibited by the geographically close *D. falcatoides*, a species with which it is almost certainly sympatric (an immature specimen possibly referable to *D. falcatoides* was also found at the above locality). Random sampling in this region has not revealed further populations of *D. lamberti*; if, as it would appear, this species is restricted to the environs of Spring Creek (an intermittent stream), one may suppose that it represents a relictual extension of a more southerly *Diploptrema* stock, now isolated because of present-day interpluvial aridity. Confirmation of this hypothesis will require more extensive sampling along the Broadsound Range and the Isaac/Mackenzie River, both of which may provide environmentally tolerable dispersal routes for earthworm populations.

### *Diploptrema longiductis* sp. nov.

(Figs 55, 56)

**TYPE LOCALITY:** N Qld, 20°14'S 148°25'E, 27 road km N of Proserpine, in sandy soil. Coll. W. Nash, 11 Jan 1975.

**HOLOTYPE:** QMGH 2913.

**PARATYPES:** QMGH 2914, ANIC GD.95.56.1.

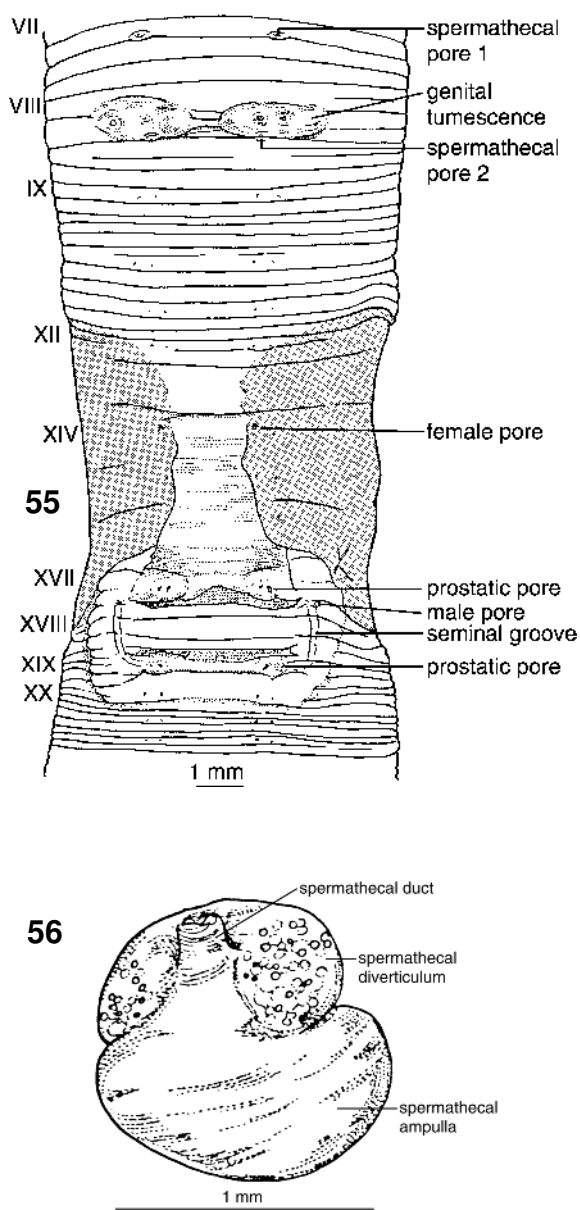
### Description

Length 91, 76+ mm. Width (midclitellar) 6.5, 7.8 mm. Segments 183, ? (H, P1 — posterior amputee). Form circular in cross-section throughout, pigmentless buff in alcohol, clitellum pinkish-brown. Prostomium prolobous, first dorsal

pore 11/12. Setae 8 per segment, commencing in II; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; those of VIII replaced by genital setae. Nephropores very rarely visible on the clitellum, well dorsal of *d*. Clitellum tumid, saddle-shaped, over ½XII–XVII, interrupted ventrally at *b* lines and the male genital field; intersegmental furrows weakly visible, dorsal pores obscured, setae obvious. Male pores quite conspicuous, often on a small papilla, immediately posteriad of intersegment 17/18, lateral of *b* setae (in some specimens, e.g. P1, the male pore is either at 17/18, or actually encroaching into XVII), in broad, arcing seminal grooves that link the prostatic porophores of a side. Two pairs of prostatic pores in XVII and XIX, on raised transverse ridges that, together with an alternating series of transverse depressions, comprise the male field; the latter extends from the setal arc in XVI to mid-XX: a prominent ridge, running across XVIII marks its midpoint, and a narrow-elliptical concavity, centred on 16/17 defines its anterior edge. The prostatic pores, coinciding with the penial seta pores, may have fine, penial setae protruding. Female pores a pair of quite prominent slits in XIV, just in front of the setal arc, slightly lateral of *a* lines. Genital markings slightly torose swellings immediately anteriad of the posterior pair of spermathecal pores, corresponding to the site of the genital setae (all specimens examined); no other genital markings detectable. Spermathecal pores conspicuous orifices surrounded by slightly tumid and puckered rims, in 7/8 and 8/9, aligned with setae *a*.

Septa 5/6 slightly thickened, 6/7 moderately so, 7/8–8/9 strongly muscularised, 9/10–10/11 only moderately augmented with musculature, remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, these, and the commissurals in XI–XII significantly larger than the remainder, and each receiving connectives from both the dorsal and supra-oesophageal vessels (the latter connectives by far the more robust); commissurals in VI–X still considerable, but dorso-ventral only; supra-oesophageal vessel seen in XI–XV. Gizzard large, muscular, cylindrical, in V, the septa 5/6–8/9 dove-tailed posteriad due to its size; a softer, anterior proventriculus present in 4/5; oesophagus quite wide, and incorporating a substantial section linking the pharynx and gizzard, which, due to the constricted space, is necessarily bent; oesophagus lacking any outpouchings or structures that may be construed as calciferous glands. Intestinal origin XVII, a definite dorsal typhlosole commencing in the region of XXVIII–XXX. Stomate, avesciculate

holonephridia present throughout, the constituent tubules of each rather elongate; nephridial ducts thin-walled, but quite wide, the site of the nephridial pore somewhat irregular, but always well above *d* lines (usually in the vicinity of the midpoint between *d* and the mid-dorsal line). Pharyngeal nephridia enlarged, but not tufted. Holandric; compacted sperm masses and 2 pairs of slightly iridescent, convoluted spermathecal funnels present in X and XI; 2 pairs of rather small, subequal seminal vesicle masses in XI and XII. Prostate glands 2 pairs of tightly coiled tubular organs, lying in their segments of origin (XVII and XIX), the anterior pair conspicuously the larger; the ducts, which are short-medium in length, lightly muscular, and with minor coiling, enter a median glandular mass (associated with the male genital field) before exiting at the porophores. Closely associated with the latter, and attached by mesentery to the glandular portion of the prostates, as well as by copulatory muscle bands to the body wall, are 2 pairs of large penisal follicles, that exceed the prostate glands in length, the anterior pair extending into XXI; these contain a large number of fine, reddish setae. The setae are very long, with a fine hair-like appearance to the naked eye, and twisting erratically when withdrawn from the penisal sheaths; under high power, the shaft is seen to be a very narrow, flattened, attenuating ribbon, that may be variously twisted and curved, the extreme ectal region (excluding the tip) ornamented with a scattering of delicate, acute spinules. Length of mature seta 9–98 mm; midshaft diameter 43.0  $\mu\text{m}$  (mean of 2). Metagynous, fairly small oocytic clusters and medium-sized plicate oviducal funnels seen in XIII, ovisacs absent. Spermathecae 2 subequal pairs, in VIII and IX; the ampulla subspherical, thin-walled, communicating through a narrow canal with a narrower diverticular region, the walls of which are considerably thicker, rugose, and studded with iridescent masses; this atrium discharges, in turn, through a rather long, sinuous, thick-walled duct. Length right spermatheca of IX (duct unravelled) = 5.9 mm (duct = approx. 1.5 times diameter of ampulla). Very large genital seta follicles present in VIII, each associated with a pair of robust, white, racemose glands: one between the nerve-cord and the follicle, the other lateral of the latter; these discharge through discrete ducts at the setal pores; each follicle is attached to the lateral aspect of the body wall by a strong retractor muscle. The setae gently curving, the ectal  $\frac{1}{3}$  with a circumferential striated appearance due to insunken, interrupted bands of small, jagged teeth that are better regimented and more densely arrayed towards the ectal end of the



**Figs 55, 56, *Diplotrema longiductis* sp. nov., Holotype.** 55, genital field; 56, left spermatheca of IX.

seta; proximally, these rows disperse, to give scattered bracts of teeth. Length of mature seta 1.51 mm; midshaft diameter 43.5 (mean of 3).

#### Remarks

*Diplotrema longiductis* is closely allied to *D. eungellae*, both species sharing the following characteristics: genital setae in VIII, the follicles



associated with prominent accessory glands; long flattened penial setae, ornamented with fine spinules; a distinctive genital field consisting of alternating ridges and depressions; seminal vesicles in XI and XII; no tufted nephridia and nephropores well dorsal of *d* lines. In *D. longiductis*, however, the male pores have migrated to the vicinity of 17/18 (equatorial in *D. eungellae*), and the spermathecal duct is dramatically more elongate. *D. conwayi*, perhaps with closer phylogenetic links to *D. longiductis* than to *D. eungellae*, nevertheless deserves inclusion in the *eungellae* species-group (genital setae with glands in VIII, seminal vesicles in XI and XII, nephropores well above *d* lines). All three species are geographically close, also suggesting derivation from common ancestral stock, perhaps in the comparatively recent past.

***Diploptrema magna* sp. nov.**

(Figs 57, 58)

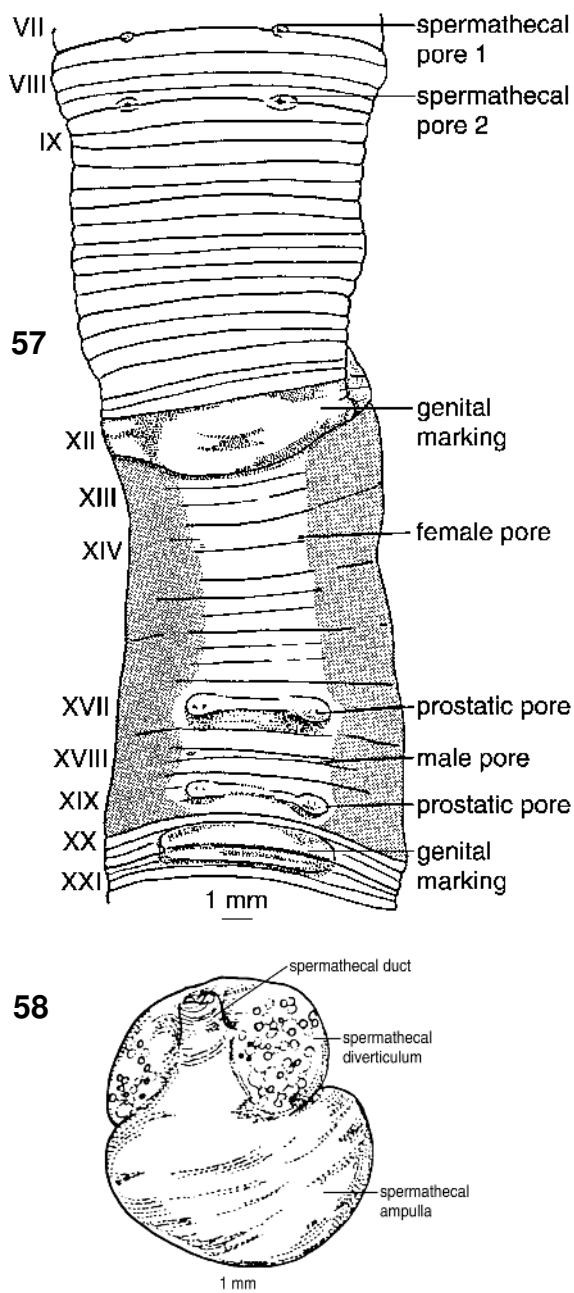
**TYPE LOCALITY:** S Central Qld, 24°12'S 150°29'E, approximately 6 km north of Bororen (10 km from Miriam Vale), at roadside, in swampy black soil near creek bridge. Coll. B.G.M. Jamieson and E. Bradbury, 21 May 1971.

**HOLOTYPE:** ANIC GD 95.61.1.

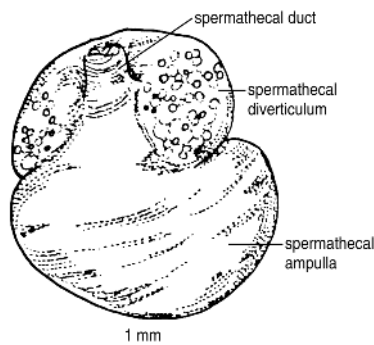
**PARATYPE:** ANIC GD.95.61.3. 2–3 paratypes.

**Description**

Length 190, 170+ mm. Width (midclitellar) 9.8, 9.1 mm. Segments, not determinable (H, PI—posterior amputee). Uniformly circular in cross-section throughout, pigmentless buff in alcohol, clitellum, when tumid, with a distinctly purplish pigmentation. Prostomium prolobous; first dorsal pore in 11/12. Setae 8 per segment, commencing on II, much reduced in size and only sporadically visible (particularly the ventro-lateral couplets, which are often only visible in sectioned preparations). Ventral setal couples consistently absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital setae lacking. Nephropores visible in the inter-segments on the clitellum just above *d* lines. Clitellum well developed, saddle-shaped, extending over XII–½XX, with a mid-ventral gap that extends across, and slightly beyond, *b* lines. Male pores visible just above *b* lines, equatorially situated in XVII, and lying in the broad seminal grooves that link the prostatic porophores of a side. Two pairs of prostatic pores present in XVII and XIX, each pore atop a small raised protrusion, with the prostatic duct apparently discharging through both of these orifices. Genital markings a series of broad, unpaired median pads extending laterally



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**Figs 57, 58, *Diploptrema magna* sp. nov., Holotype. 57, genital field; 58, right spermatheca of IX**

beyond *b* lines: one fills segment XII and extends a little into XIII; the other two are intersegmental, in 20/21 and 21/22, though sufficiently broad to be in contact across XXI. Marking in 21/22 seen in

Holotype, P3 and P5 only, the other markings present in all specimens examined. Female pores a pair of orifices in front of the setal arc in XIV, slightly lateral of *b* lines. Spermathecal pores 2 pairs in 7/8 and 8/9, aligned with setae.

Septa 5/6–9/10 strongly muscularised and thickened, 10/11 moderately so; septum 11/12 partially aborted, enclosing segment XI in a diaphanous pericardial sac (i.e. 11/12 is not attached to the dorsal body wall, but is attached to the posterior face of 10/11. Septa 5/6–10/11 deflected posteriorly owing to the bulk of the gizzard. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; commissurals in X–XIII large, valvular, and heart-like, receiving connectives from both the dorsal and supra-oesophageal vessels (the connectives from the latter vessel being the more substantial); remaining commissurals decreasing in size anteriorly, and dorsoventral only. Supra-oesophageal apparently restricted to X–XIII, a conspicuous major lateral vessel, supplying the body wall and septa, is visible arising from the ventral vessel, in XIV. Gizzard large, firm (muscular) and barrel-shaped, in V, with a much dilated and coiled, thin-walled oesophageal portion between pharynx and gizzard proper; posterior section of the gizzard seems firmer; oesophagus rather wide, somewhat truncated anteriorly due to the size of the gizzard, lacking any definite pouching or calciferous glands, extending from VI to XVI. Intestine commences abruptly in XVII, a well-developed dorsal typhlosole present. Holonephric; each nephridium with a rather small preseptal funnel, not much larger than the neck, and a long, avascular duct entering the parietes at a point difficult to define due to the virtual lack of somatic seta development, but presumed, from position of the pores externally, to be near *d*. Pharyngeal tufting absent. Metandric; a single, very large pair of spermathecal funnels that are brightly iridescent and convoluted, in XI; a single pair of very large, lobulated seminal vesicles composed of fine loculi adherent to the posterior face of septum 11/12. Prostate glands pairs of tubular, highly coiled organs restricted to their segments of origin (XVII and XIX); ducts moderately short, and not highly muscular; the anterior pair of prostates is conspicuously the larger; the ducts are associated with moderately large penial setae of varying dimensions, the more immature shafts being distinctly reddish in colour; the follicular 'pouch' is in all cases, ligamentated by a narrow muscular band to a point close to the mid-dorsal line; the area immediately surrounding the porophore is also provided with

copulatory musculature. The setae describing rather gently curving arcs (often with a right-angle twist, ectally); the extreme tip may be bent or relatively straight; the shaft is devoid of any toothing, but the upper midshaft may be dimpled in appearance, due to scattered, shallow, narrow notches. Length of mature seta 4.94 mm; midshaft diameter 46.9  $\mu$ m (mean of 3). Ovaries quite small, but large, plicate, oviducal funnels present in XIII, ovisacs absent. Spermathecae 2 pairs in VIII and IX, discharging anteriorly in their respective segments; each is a bilobed organ, consisting of a posteriorly directed bulbous ampulla, joined by a wide waist to an equisized 'diverticulum' containing many iridescent intramural sperm chambers. The diverticulum overhangs the short duct *in situ*; the ampulla, which contains a whitish coagulum, communicates to the duct via the 'diverticulum'. Length of right spermatheca of IX 3.9 mm. Genital seta follicles absent.

### Remarks

*Diplotrema magna* is readily characterised by its large size, the metandric condition of its gonads, and the absence of genital setae. There are some points of resemblance with the more northerly *D. boardmani*, including the presence of accessory genital pads in 20/21 and 21/22, and similar construction of the spermathecae, though in view of the size discrepancy and fixation of metandry in *D. magna*, the relationship between the two species is considered tenuous. Another member of the *D. boardmani* species-group, *D. bulburinensis*, does exhibit metandry (as well as markings in 20/21 and 21/22, and similar spermathecae), so that the inclusion of *D. magna* in this assemblage little affects its homogeneity.

### *Diplotrema magnetis* sp. nov.

(Figs 59, 60)

**TYPE LOCALITY:** Qld, 19°07'S 146°49'E, Horseshoe Bay, Magnetic Island, near Townsville, NQ., in a moist gully, black loam. Coll. D. Lambert, 10 Feb 1975.

**HOLOTYPE:** QMGH 2911.

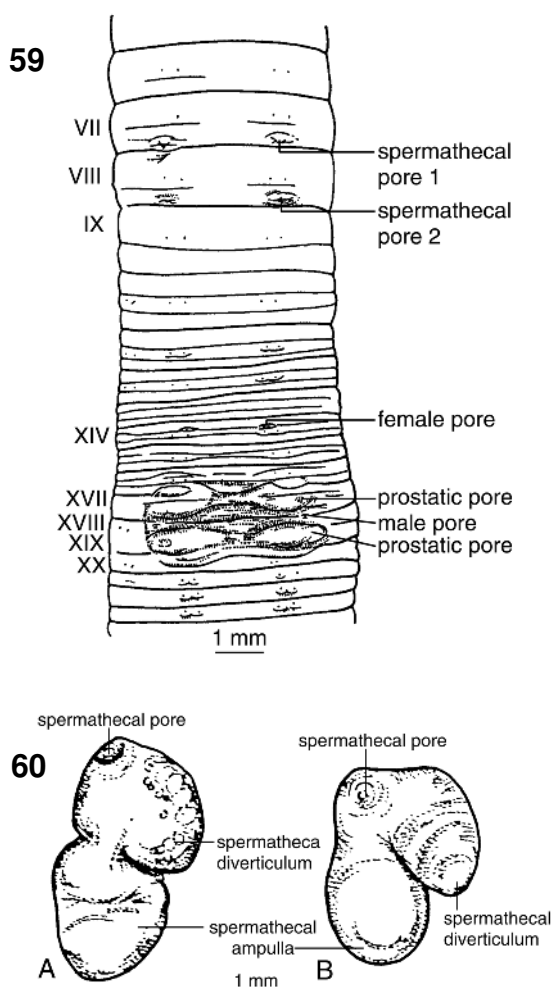
**PARATYPE:** QMGH 2912.

### Description

Length 83, 66 mm. Width (midclitellar) 4.8, 4.9 mm. Segments 244, 129 (H, P1). Uniformly circular in cross-section throughout, brownish due to initial preservation in methylated spirit; prostomium epilobous 1/2, closed. First dorsal pore in 11/12. Setae 8 per segment, in uniform rows throughout; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; genital setae lacking.

Nephropores seen as distinct whitish spots on the clitellum, apparently alternating regularly between a point just below *c* lines to one well above *d*, closer to the mid-ventral line than to *d*. Clitellum not strongly developed, extending over ½XIII–XIX (saddle-shaped); dorsal pores, inter-segmental furrows and setae obvious. Male pores conspicuous slits lateral of *b* lines, at the extreme anterior portion of XVIII, bordering on XVII; seminal grooves not detected. Prostatic porophores conspicuously projecting in segments XVII and XIX, their relief accentuated by the concavity that separates all four porophores. A very narrow, slightly raised strip on which the male pores are located, passes through the latter depression. Genital markings a single pair of small, elliptical swellings immediately anterior to the porophore mounds of XVII (located between these and the ventral setal couples of XVI). No other accessory markings detectable. Female pores a pair of minute orifices in XIV, on glandular surrounds, slightly presetal, in *a* lines. Spermathecal pores 2 pairs aligned with *b* setae in 7/8 and 8/9.

Septa 5/6 unthickened, 6/7 slightly thickened, 7/8 moderately muscularised, 8/9–10/11 strongly so; septum 11/12 membranous, partially aborted, attached dorsally (below the dorsal blood vessel), and laterally to the posterior face of 10/11, effectively encapsulating most of the organ systems of XI, and producing an internal pseudosegmentation. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; those in XII considerable, XI diminutive in comparison; only the former pairs of commissurals receiving connectives from both the dorsal and supra-oesophageal vessels; remaining commissurals, though quite robust, are dorsoventral only. Supra-oesophageal vessel present in X–XIII. Gizzard dolioform, large, shiny, and muscular, in V; the oesophagus rather narrow, but dilated in XII–XIII into pouch-like projections, which, in possessing well-developed internal lamellae, might be considered sessile calciferous glands; intestinal origin in XVIII; a low, dorsal typhlosole commencing in XIX. Holonephric throughout; each segment with a pair of simple, stomate nephridial bodies, the avesiculate ducts of which alternate regularly in their position of entry into the parietes, between mid *bc*, and a point far dorsal of *d*. Pharyngeal nephridial bodies enlarged, but no tufting demonstrable. Metandric; the posterior pair of testes and spermathecal funnels (in XI) retained only, and these are enclosed by the peculiar septal arrangement described above. The spermathecal funnels are very large, brightly iridescent, and associated with dense sperm masses. A pair of very large, finely loculated seminal vesicle masses



**Figs 59, 60, *Diploptrema magnetis* sp. nov.** 59, genital field of Holotype; 60: A, right spermatheca of IX, Holotype; B, right spermatheca of IX, Paratype 1.

present in XII; vasa deferentia readily seen, at first fairly straight, not attached to the body wall for several segments, becoming sessile and tortuous in XIII; thence the vasa deferentia loop under the prostatic ducts in XVII, to enter the body wall at 17/18, now an apparently muscular, somewhat thickened duct. Prostate glands 2 pairs of coiled tubular structures in XVII and XIX, with short, muscular ducts; associated with the latter are medium-sized penisetal follicles, each containing a number of setae; the setae moderately long, a small section (approx. 1/8) with irregular clusters of small toothlets (varying in density) near the distal end; this is followed by a smooth section of approximately the same length, just before the tip,

which, invariably, is strongly recurved (giving an uncinate appearance). Length of mature seta 2.29 mm; midshaft diameter 40.0  $\mu$ m (mean of 3). Palmate oocytic clusters and small oviducal funnels seen in XIII. Spermathecae 2 subequal pairs in VIII and IX, each consisting of a sacciform ampulla, with a narrow neck that is all but embedded in a broad U-shaped diverticulum (with internal iridescence); both components share a very short duct. Length right spermatheca of IX = 2.0 mm. Genital setae lacking. In the sole paratype, the calciferous gland elaborations lie in XIII–XIV; the spermathecae are of a somewhat different construction, having a diverticulum of similar shape and proportions as the ampulla.

### Remarks

As Dyne (1984) notes, this species exhibits a dramatic departure from what is considered to be the ancestral morphology of the proto-*Diploptrema* stock. The following apomorphic character states define the species: lack of genital setae, development of calciferous glands (or the homologues thereof), regular nephropore alternation, reduction of the male system to the metandric condition. The species thus occupies a somewhat isolated position within *Diploptrema*, though there may be some affinity with the nearby mainland *D. heteropora* complex.

### *Diploptrema montislewisi* sp. nov.

(Figs 61, 62)

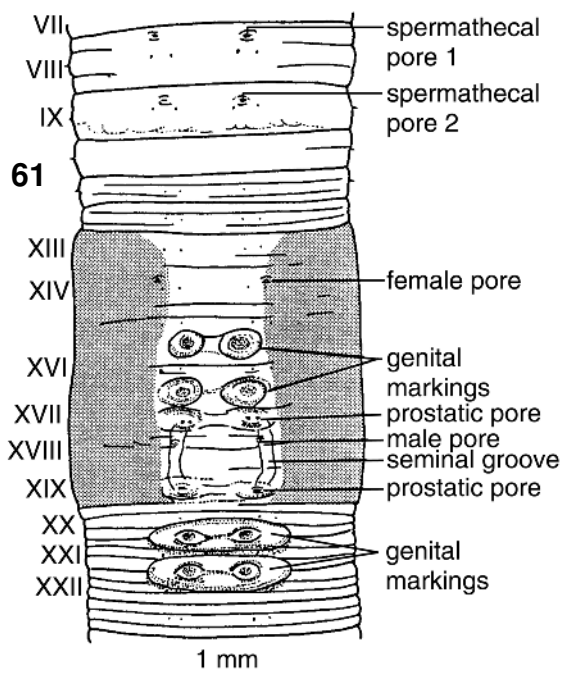
**TYPE LOCALITY:** N QLD, 16°34'S 145°17'E, Mt Lewis, under rocks in wet mesophyll vine-forest at the summit; soil parent material granites and schists. Coll. T. Walker, 27 May 1972.

**HOLOTYPE:** QMGH 2921.

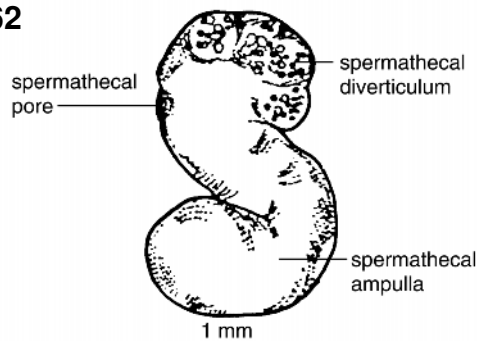
**PARATYPE:** Lodgement unknown.

### Description

Length 48, 35 mm. Width (midclitellar) 2.6, 2.5 mm. Segments 148, 180 (H, P1). Form circular in cross-section throughout, pigmentless grey-buff in alcohol. Prostomium epilobous 1/3, closed; first dorsal pore 12/13 (H, P1). Setae in 8 regular, longitudinal rows throughout, commencing on II; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; genital setae absent. Nephropores not externally recognisable. Clitellum tumescent, saddle-shaped, over XIII–XIX; dorsal pores, intersegmental furrows obscured; clitellum interrupted ventrally at *b* lines. Male pores minute, in *ab* (closer to *b*), presetally situated in XVIII, in shallow seminal grooves; the latter are broad, and fairly straight, linking the prostatic pores of a side. Prostatic porophore mounds slight, no protuberant setae seen. Genital markings paired, conjoined, elliptical



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**Figs 61, 62, *Diploptrema montislewisi* sp. nov., Holotype.** 61, genital field; 62, right spermatheca of VIII.

tumescences with oculate centres present in 15/16, 16/17 (approximately confined within *bb*), and a similar, more protuberant pair in 10/21, 21/22. In P1, an additional marking is present in 22/23. Female pores recognisable slits at the margins of the clitellum, pre-setally situated on XIV, in *b* lines. Spermathecal pores 2 pairs, intra-segmental: in VIII midway between the setal arc and intersegment 7/8 (in *ab*, closer to *b*), and in IX just anteriad of the setal arc.

No septa strongly muscularised, though most septa anterior to 12/13 are slightly thickened (7/8 and 8/9 perhaps the most robust). Dorsal blood vessel single; last hearts in XIII; only these commissurals and those of XII of sufficient size to be termed hearts, though those of XI are quite large. Further details of the blood system not determinable due to extensive bleaching. Gizzard moderately large, though compressible, in V. Oesophagus moniliform, in VI–XVI, with conspicuous, internally lamellate, reniform calciferous glands arising ventro-laterally on thin stalks, in XII–XV. Intestine commences in XVII, a very strongly developed, bipartite typhlosole abruptly commencing on the roof of the intestine in XX, and extending ventrally for nearly the diameter of the intestine. Holonephric; 2 pairs of medium-sized, iridescent spermatid funnels present in X and XI, with acinous seminal vesicles in IX and XII. Prostate glands 2 pairs of tortuous tubular organs, in XVII and XIX, restricted to these segments, the anterior pair larger and more highly coiled; ducts thin and straight. Rather small penisetal follicles associated with the ducts, have substantial retractor ligaments; the setae gently curving, entire (lacking any form of regular ornamentation). Length of mature seta 1.38 mm; midshaft diameter 26.5µm (mean of 3). Ovaries visible as conjoined oocytic strings, together with medium-sized, plicate oviducal funnels, in XIII. Spermathecae 2 pairs, discharging intrasegmentally, in VIII and IX (the posterior set the larger); each consisting of a pyriform ampulla and distinct reniform diverticulum fusing to discharge through a very short duct; diverticulum often packed with iridescent sperm chambers; alternatively, the diverticulum may be quite short, partially surrounding the duct, and accompanied by a long ampulla (as in right VIII of H). Length right spermatheca of IX = (base of ampulla to pore) 1.0 mm.

### Remarks

This small species is readily diagnosed by the combination of presence of intrasegmental spermathecal pores, a series of distinct genital markings, and stalked calciferous glands in the oesophageal region.

### *Diploptrema narayensis* Blakemore, 1997

*Diploptrema narayensis* Blakemore, 1997: 1799–1802, fig. 5.

**TYPE LOCALITY:** QLD, 25°44'S 150°46'E, CSIRO Narayan Research Station, near Mundubbera.

**HOLOTYPE:** ANIC RB.94.7.7.

**PARATYPES:** ANIC RB.94.7.8–94.7.14.

### Description (after Blakemore 1997)

Length 33–45 mm. Width 1.5–2.5 mm. Segments 90–104 (segment VIII sometimes thicker and more tumid). Unpigmented; anterior faint pink with blue iridescence; clitellum buff. Prostomium propilobous appearing closed epilobous when forced back by pharynx eversion on preservation. First dorsal pore 7/8 (or 8/9), not obvious except on clitellum. Setae minute and closely paired, 8 per segment from II, ventral setae absent on XVIII; genital setae small on VIII, larger on IX; penial setae [undescribed] large on XVII, smaller on XIX, silvery more often than red. Mean setal ratios 6: 1: 6: 1: 20: 0.5. Nephropores minute in *cd* lines. Clitellum XIII–XVII, annular excluding male field. Male pores minute in XVIII in slightly outwardly bowed seminal grooves between pairs of prostates equatorial in *ab* in XVII and XIX; whole field depressed between the grooves with raised setal and genital papillae. Genital markings: genital setae on small tumescences on VIII and IX; paired ventral markings on small raised pad in 16/17 (as wide apart as prostatic tumescences in some specimens); narrower pairs in 17/18 and 18/19 and a further pair in a ventral tumid pad in 19/20 (this last pair often fainter than anterior pairs). Female pores in XIV, minute, anterior to *a* setae. Spermathecal pores 2 pairs, in 7/8 and 8/9 ventral in *ab* lines.

Septa 6/7–9/10 moderately thick, 5/6 and 10/11–12/13 weak. Dorsal blood vessel: single, continuous onto pharynx (ventral vessel paired under gizzard). Last hearts in XIII (found on right side only in some) or in XII in one specimen. Gizzard: in V displaced posteriorly, muscular (with proventriculus in IV). Calciferous glands absent but oesophagus dilated in VII–XII. Intestine from XV; typhlosole absent but low dorsal ridge from XXIV. Gut contents: mainly colloidal soil plus some dark organic debris. Nephridia holonephridia, not tufted anteriorly. Holandric, iridescent funnels in X and XI; seminal vesicles racemose in IX posteriorly, and larger in XII anteriorly. Ovaries large palmate pair each with 3–4 egg strings, in XIII. Two pairs of elongate convoluted tubular prostates with short muscular ducts in XVII and XIX, interlocking on each side, each gland extending back two or three segments; long penial setae sheaves [setae undescribed] converge with ducts. Spermathecae two pairs in VIII and IX, form slightly variable, mostly with yellow spherical or clavate ampulla on short duct and larger tongue-like diverticulum containing several iridescent 'strings'. In some specimens ampullae and diverticula of equal size, or with

more elongate diverticula, those in IX larger than those in VIII. Ampullae overlie the ensheathed genital setal bundles.

### Remarks

Blakemore (1997) notes that *Diploptrema narayensis* is close, both morphologically and in geographical distribution, to the similarly small *Diploptrema fragilis* which Spencer (1900) found at Gayndah and Cooran. Especially similar are the (depressed) glandular patches extending over XVI–XIX, which in *D. fragilis* are marked with ventral pads in 18/19 and 19/20 as in this species. However, he states that *D. narayensis* can be separated from *D. fragilis* by absence of ventral setae on XVIII; absence of glandular swelling of VIII (in most specimens); presence of ventral markings in 16/17; seminal vesicles in IX and XII (rather than XII only [Spencer], or, it is here added, XI and XII); prostates of equal rather than subequal size and by the absence of latero-neural glandular mass (ventral glands *sensu* Dyne and Jamieson 1997) internally in XVII–XIX (in most specimens, although one did have this glandular mass). It will be noted that these differences are sometimes not complete and none is substantial. Blakemore notes that *D. narayensis* is remarkably similar to *D. capella*, which was found in a comparable habitat 300 km NW of Narayen. As noted in its description, *D. capella* is morphologically close to *D. tyagarah* from NSW. *D. narayensis* differs from this latter species for parallel reasons. These three species may, nevertheless, form a complex with *D. fragilis* (see Blakemore 1997).

Blakemore (1997) discusses the agronomic potential of *D. narayensis*.

### *Diploptrema nemoralis* sp. nov.

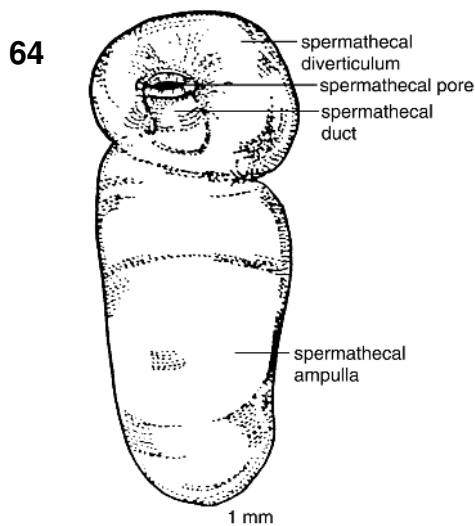
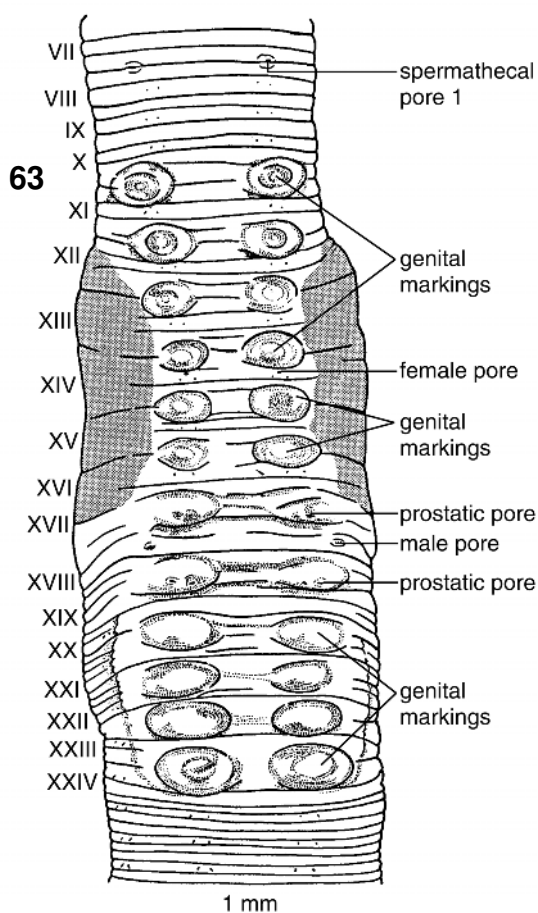
(Figs 63, 64)

**TYPE LOCALITY:** QLD, 21°08'S 148°30'E, Broken River, Eungella National Park. Coll. G. Dyne and A. Postle, 13 Jun 1974.

**HOLOTYPE:** QMGH 2894.

### Description

Length 153.5 mm. Width (midclitellar) 5.7 mm. Segments 237. Form circular in cross-section throughout, pigmentless buff in alcohol, clitellum with a pinkish tinge. Prostomium prolobous; first dorsal pore 11/12. Setae 8 per segment, in regular longitudinal rows throughout; ventral setal couples of XVIII lacking; those of XVII and XIX modified as penial setae; genital setae absent. Nephropores visible in the clitellar region as small, whitish, intersegmental marks; rather irregularly disposed, but all well above *d* lines. Clitellum tumid, saddle-shaped, over XII–XVII. Male pores quite



**Figs 63, 64.** *Diploptrema nemoralis* sp. nov. Holotype. 63, genital field; 64, right spermatheca of IX.

conspicuous, on slight papillae, lateral of *b* lines, equatorially situated in XVIII. Prostatic pores on large, transversely elliptical mounds in XVII and XIX, coinciding with the setal pores, though no penial setae were seen to protrude externally; the pores of a side are joined by an extremely faint seminal groove. The posterior edge of the prostatic porophores mounds are accentuated by concavities immediately posteriad. Genital markings a series of paired, intersegmental, transversely elliptical pads (with dome-shaped, glandular centres), present in 10/11–15/16; a further series of slightly broader pads is present in 20/21–23/24. All pads are centred on *ab*. Female pores seen as slits presetally (in *ab*), on XIV. Spermathecal pores 2 pairs with tumid lips, in 7/8 and 8/9, in *b* lines.

Septa 5/6 delicate, 6/7–8/9 with slight to moderate muscular thickening 9/10 clearly the most robust septum, 10/11–11/12 weakly muscularised. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; commissurals gradually diminishing in size anteriorly (though no commissural is conspicuously much larger than the rest); at least the three posteriormost commissurals are latero-oesophageal, receiving connectives from both the dorsal and supra-oesophageal vessels; supra-oesophageal vessel substantial, rivalling the dorsal vessel in size, seen in X–XIV. Gizzard a very large, muscular, cylindrical organ, in V; oesophagus of fairly uniform diameter, in VI–XVI, lacking elaborations of any kind; intestine commences in XVII, a definite dorsal typhlosole developing in XXIX, with gradual enlargement posteriad. Nephridia simple, paired loops throughout, commencing in II; the avesiculate ducts do not discharge in a uniform manner, but do open consistently well above *d* lines. Nephrostomes of the nephridial bodies in the intestinal region large and conspicuous, attached to delicate necks slightly ventral of *a* lines; anterior tufted nephridia absent. Holandric; 2 pairs of medium-large iridescent spermathecal funnels present in X and XI; 2 pairs of fairly large seminal vesicles, containing loculi of varying size, present in XI and XII; vasa deferentia readily seen as paired, iridescent tubes winding tortuously on each side of the oesophagus, remaining unfused except at the male pore itself. Prostate glands 2 pairs of elaborately coiled organs with sinuous, muscular ducts entering the parietes through the *b* penisetal orifices, in XVII and XIX; the glandular portions of the prostates are not confined to the above segments, and appear roughly square in cross-section; general copulatory musculature associated with the male genital field well developed, particularly in XVIII. Very large penisetal follicles are associated with, and attached by mesentery to

the prostate glands; these are also provided with robust extensor and retractor musculature, inserted on the body wall. The setae contained within the follicles are very long, rather flat, and strongly curving, the extreme ectal portion of the shaft (excluding the region immediately below the tip) ornamented with rows of narrow, sharp teeth that are closely adpressed to the surface. Length of mature seta 4.21 mm; midshaft diameter 61.7  $\mu$ m. Small cuneiform ovaries and medium-sized translucent funnels present in XIII. Spermathecae 2 pairs in VIII and IX, the posterior pair the larger by a small margin. Each organ is composed of a fairly long, tubulo-sacciform ampulla, and bulbous, inseminated diverticulum, from the middles of which a short duct arises. Length right spermatheca of IX = 2.9 mm (base of ampulla to pore).

### Remarks

*Diploptrema nemoralis*, sympatric with *D. eungellae* over at least a portion of its range, is apparently rare; only a single specimen was forthcoming from an extensive sampling programme in the Eungella area that yielded numerous specimens of other earthworm species. It is characterised by a striking series of bold genital accessory markings in 10/11–15/16 and in 20/21–23/24, absence of genital setae, and location of seminal vesicles in XI and XII. The affinities of *D. nemoralis* are uncertain.

### *Diploptrema peraeintestinalis* sp. nov.

(Figs 65, 66)

**TYPE LOCALITY:** Qld, 17°01'S 145°45'E, White Rock Mountain, in rainforest, halfway to summit. Coll. W. Nash and M. Shand, 8 Jan 1975.

**HOLOTYPE:** Lodgement unknown.

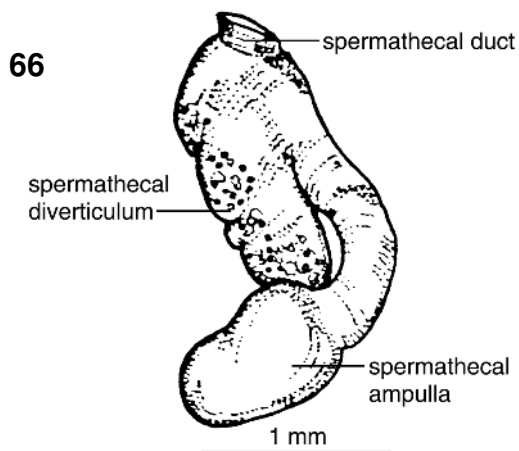
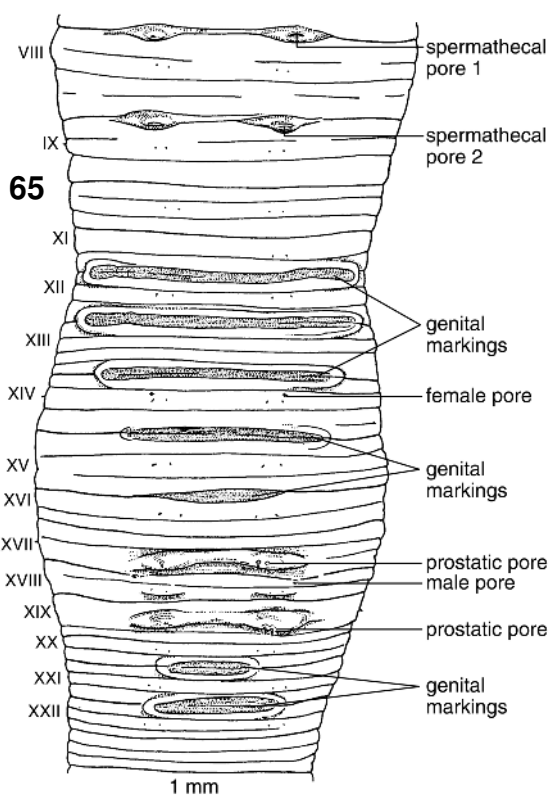
**PARATYPE:** Lodgement unknown.

### Description

Length 131, 81+ mm. Width (midclitellar) 4.9, 3.9 mm. Segments 272, ? (H, P1). Body uniformly circular in cross-section throughout, bulging in the clitellar region, a dull whitish colour in alcohol. Prostomium prolobous; first dorsal pore 9/10 (H, P1). Setae 8 per segment; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; genital setae lacking. Nephropores visible on small, but conspicuous papillae on the clitellum, and as obvious openings in the forebody, in *d* lines. Clitellum pigmented, tumid, over XIII–XVIII, saddle-shaped, though its lateral limits are not determinable; the clitellum is certainly better developed dorsally, though setae, intersegmental furrows and dorsal pores are not obscured. Male pores seen as small orifices, barely within XVIII, at 17/18, lateral of *b* lines by a distance equal to *ab*; seminal grooves indistinct;

prostatic porophores 2 pairs, in XVII and XIX, the small mounds of a pair conjoined by a tumid ridge that overhangs a furrow immediately posteriad. Genital markings a series of long, narrow, intersegmental markings, with depressed, glandular centres and raised rims well-defined by a deep furrow, present in 11/12–14/15. These extend laterally beyond *b*, but decrease in length posteriad; a shallow, poorly defined marking is present in 16/17 anterior to the porophore mounds; 2 further intersegmental markings are present in 20/21 (confined within *aa*), and 21/22 (extending across *bb*). All mature or semi-mature specimens examined exhibit the above markings, though they may be only faintly developed in some individuals. Female pores a pair of small, presetal slits in IV, just lateral of *b*. Spermathecal pores 2 obvious pairs of openings in the intersegments 7/8 and 8/9, in *b* lines.

Septa 5/6, 6/7 thin, 7/8, 8/9 moderately muscularised; 9/10 and 11/12 fused, encapsulating segments X and XI; septum 10/11 very weak (i.e. segments X and XI poorly partitioned). Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; commissurals in the latter segment and XII the only large, heart-like units, receiving connectives from both the dorsal and supra-oesophageal vessels; the latter is very strongly developed in XI–XIV, contributing latero-oesophageal trunks to the highly vascularised oesophagus. Gizzard of moderate size, firm, globose, in V, not impinging on segments posteriad of 6/7; oesophagus moniliform, well supplied with blood vessels, in VI–XVI; in X–XV with well-defined ventro-lateral diverticula (those in X and XI short and virtually sessile; those in XII–XV well-demarcated sacciform projections with internal lamellae). Intestine commences abruptly in XVII; a low dorsal typhlosole commencing in XXII. Holonephric; stomate, avesiculate nephridia with thin-walled ducts present throughout; the ducts entering the parietes in *d* lines. Anterior tufting not demonstrable. Holandric; 2 pairs small-medium, lightly iridescent funnels present in X and XI; 2 pairs of seminal vesicles adherent to septa 9/10 and 11/12 present in IX and XII respectively; vasa deferentia clearly visible as iridescent strands winding on the body wall. Prostate glands 2 pairs of coiled, tubular organs, the posterior pair quite small, ?rudimentary; ducts fairly short and straight. Penisetal follicles developed only to a moderate size, and containing numerous, fairly short setae; the setae are conspicuously flattened, the tips gently rounded, and very slightly bent; no ornamentation present on the shaft; length of mature seta 1.74 mm; midshaft diameter 37.3  $\mu$ m (mean of 3). Small



**Figs 65, 66.** *Diplootrema peraeintestinalis* sp. nov., Holotype. **65**, genital field; **66**, right spermatheca of IX.

oocytic clusters and simple funnels present in XIII, ovisacs absent. Spermathecae 2 pairs, the posterior pair obviously the larger. Each consists of a fairly long, digitiform ampulla (with or without a



terminal bulb), with an inseminated diverticulum, which may be in the form of a discrete tubular sac, or a flattened, reniform structure partially surrounding the duct; the latter is rather short. Length right spermatheca of IX = 2.8 mm (apex of ampulla to pore). Genital setae absent.

#### Remarks

As type specimens cannot be located, this species is erected on the illustration and account in Dyne (1984, unpublished) (ICZN 1999: Art. 73.1.4.).

In many respects, *Diploptrema peraeintestinalis* might be considered an intermediate between the microscolecin *D. glandifera* and its acanthodrilin relatives. The features it has in common with *D. glandifera* are as follows: discrete, lamellated gut diverticula, nephropores in *d* lines, broadly flattened penial setae, similar spermathecal construction, and lack of genital setae. With the exception of the last character, *D. athertoni* might also be included in this comparison, though *D. peraeintestinalis* has the additional feature of much reduced posterior prostates (and correspondingly diminished anterior spermathecae). The testis-sac-like elaboration of the septa in 9/10–11/12 also parallels the condition seen in at least one population of *D. glandifera*. The transition to the microscolecin condition would appear to be a gradual one, involving a reduction in size and function of the posterior prostates, which is accompanied by an anterior shifting of the male pore, and a diminution in importance of the anterior set of spermathecae; if the step were more saltatory, one would not expect forms intermediate in morphology, such as *D. peraeintestinalis*. All three species mentioned above are doubtless derived from a common, possibly more widespread, ancestral stock, and in the variability of their organisation, reflect the differential selection pressures that have acted on separate demes of that stock.

#### *Diploptrema proserpinensis* Dyne and Jamieson, 1998 (Figs 67, 68)

*Diploptrema proserpinensis* Dyne and Jamieson, 1998: 491–493, fig. 4,5.

**TYPE LOCALITY:** Qld, 20°23'S 148°36'E, Myrtle Creek, between Cannonvale and Proserpine; common in mud in the bottom of and in the bank of a stagnant backwater. Coll. B.G.M. Jamieson.

**HOLOTYPE:** QM G5449.

**PARATYPES:** QM G2887, 2892, 2893.

**OTHER MATERIAL:** QML GH12888.

#### Description (after Dyne and Jamieson 1998)

Length 82–103 mm. Width 1.5 mm. Segments 175–225. Form cylindrical, anterior end slightly bulbous over several segments, pale in alcohol. Prostomium pro-epilobous; dorsal pores absent. Setae closely paired throughout; ventral setal couples of XVIII present; those of XVII and XIX modified as enlarged penial setae, often protruding through the prostatic pores; those of VIII replaced by genital setae, situated on strongly protuberant papillae. Nephropores not externally recognisable. Clitellum not developed. Male pores seen slightly presetally, lateral of *b* lines, in shallow seminal grooves that link the porophores of a side; prostatic pores 2 pairs, on medially inclined dome-shaped papillae at the *ab* loci of XVII and XIX. The ventral body surface is depressed within the area circumscribed by the 4 prostatic papillae and extending as far as intersegment 16/17 and 19/20; its margins raised on each side as a longitudinal ridge along which the seminal grooves run. Genital marking a large, glandular pad, approximately circular in outline occupies most of XX between the *a* setae, and encroaches somewhat into XIX; but may be weakly developed or absent. Female pores minute, presetal in *a* or *b* lines of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, seen as elliptical areas, in *b* lines.

Septa none strongly muscularised, but those anterior to and excluding 9/10 somewhat thickened. Dorsal blood vessel single; last hearts in XIII; of all the commissurals in VII–XIII, only those in XII and XIII are large and heart-like; further vascular details not determinable due to the small size of the species and pronounced fading. Gizzard rather large, in V; oesophagus narrow, moniliform, in VI–XIX, lacking pouching or calciferous glands. Intestine commences in XIX or XX, a well-developed oesophageal valve present at 18/19 or 19/20; typhlosole absent. Nephridia present at least as far forward as VIII, stomate, their avesiculate ducts entering the parietes in a single series on each side, in *c* lines; pharyngeal tufting absent. Holandric; 2 pairs of very large, iridescent spermathecal funnels, and sperm masses, free in X and XI; seminal vesicles lobed, in XI and XII, those of XII filling the segment longitudinally, those of IX smaller. Prostate glands slender tubes; those of XVII slightly tortuous, and extending into XIX or XX; those of XIX much smaller, tortuous, extending into XX; each with a slender duct. Penisetal follicles well developed, each extending into its next posterior segment, 4 or more setae to a bundle. The setae curved gently, or through as much as a semicircle; ornamented over the distal sixth by a series of widely separated, minute, distally directed teeth, some or all of which are members of transverse circlets; the

of 3); midshaft diameter 27.3  $\mu\text{m}$ . Ovaries, each with several strings of large oocytes, and funnels, present in XIII, ovisacs absent. Spermathecae 2 pairs, in VIII and IX, the posterior pair almost twice as large as the anterior. Each with a large, somewhat irregular ampulla, and a stout duct, at the ectal end of which, medially, is a single, large, ovoid diverticulum, which may be almost as large as the ampulla. Length left spermatheca of IX = 0.66 mm.

#### Remarks

Like *Diploptrema helonoma*, and the Western Australian species, *D. cornigravei*, *D. proserpinensis* has adopted a semi-aquatic mode of existence, thus occupying a niche not yet fully exploited by other Australian acanthodrilids. Both the latter two species lack dorsal pores, a somewhat rare condition within the Megascolecidae. Absence is presumed to be a secondary loss associated with their amphibious habits, a phenomenon also seen in the primarily limnic families Almididae, Biwadrilidae, Lutodrilidae, Sparganophilidae and the marine littoral megascolecid *Pontodrilus litoralis*. Loss is presumably a response to the lack of a requirement for lubrication by expelled coelomic fluid in aquatic habitats. The loss of dorsal pores in *D. cornigravei*, recorded from 'swampy ground' (Jackson 1931), has presumably occurred independent of loss in *D. proserpinensis*, as the two species do not seem closely related.

Whereas the gut contents of *D. helonoma* consisted almost entirely of soft, partially digested organic matter, the upper alimentary tract of *D. proserpinensis* was found to contain numerous irregular quartz grains (especially in the gizzard). This may explain the differential development of the gizzard in the two species (Dyne and Jamieson 1998).

#### *Diploptrema quasifragilis* sp. nov.

(Figs 69, 70)

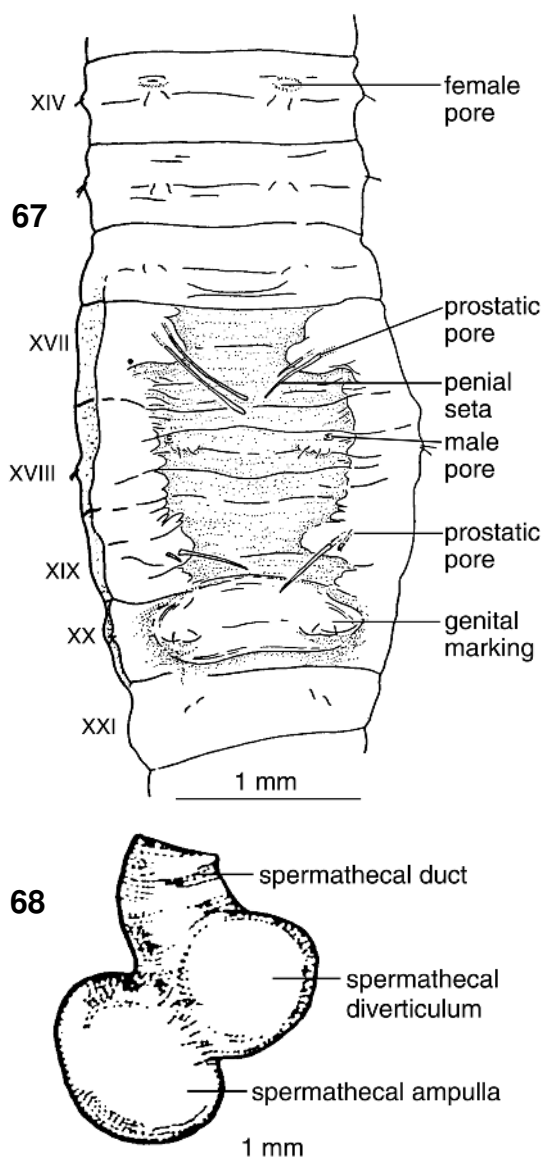
**TYPE LOCALITY:** QLD, 2830'S 15027'E, 17.5 km NE of Goondiwindi, via Cunningham Highway, in muddy black soil, about 3 metres from the edge of a shallow waterhole in cleared grazing country. Coll. R. Raven and W. Nash, 20 July 1975.

**HOLOTYPE:** Lodgement unknown.

**PARATYPES:** (20 specimens), lodgement unknown.

#### Description

Length 47, 44.5 mm. Width (midclitellar) 2.3, 2.2 mm. Segments 114, 113 (H, P1). Form circular in cross-section throughout, brownish (artefact?) in alcohol. Prostomium epilobous 1/2, closed. First dorsal pore 11/12–12/13 (apparently variable). Setae prominent, closely paired, commencing on

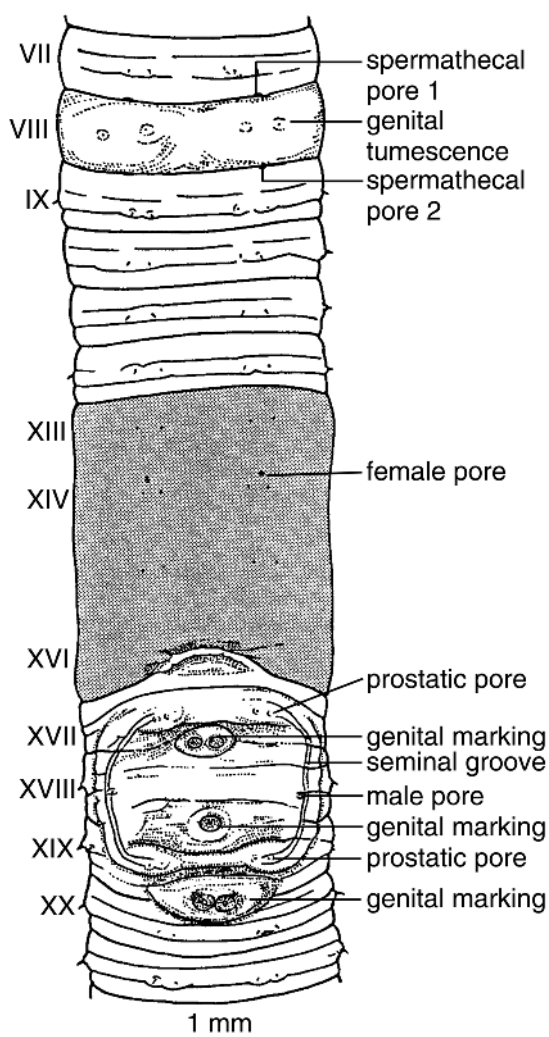


**Figs 67, 68, *Diploptrema proserpinensis* sp. nov.** Holotype. 67, genital field; 68, left spermatheca of IX.

distal extremity of the seta 'laterally' widened, and terminally forming a bulb with or without a small, apical point. Length of mature seta 0.75 mm; midshaft diameter 27.3  $\mu\text{m}$  (mean of 2). Large genital seta follicles present in VIII, apparently associated with a glandular manifestation; the setae fairly straight, the ectal 1/3 ornamented with a series of longitudinal scallops, giving a serrated appearance. Length of mature seta 0.75 mm (mean

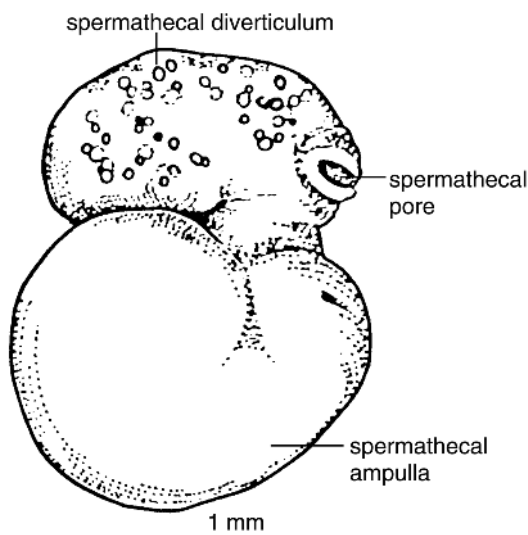
II; ventral setal couples of XVIII absent; those of XVII and XIX modified as penial setae; those of VIII modified as genital setae. Nephropores sporadically visible in the clitellar region, intersegmentally, approximately aligned with *d* setae. Clitellum tumid, saddle-shaped, over XIII–XVI, encroaching on XVII dorsally; setae, intersegmental furrows obscure, dorsal pores occluded. Male pores barely visible as minute points just anterior to the setal arc, lateral of *b* lines, in XVIII; these lie in narrow, though distinct, seminal grooves that join the prostatic porophores of a side. The male field consists of 3 major ridge lines, interspersed with concavities; the former consist of a pair of parenthesis-shaped, narrow, tumid strips bowed laterally, that incorporate and connect the porophore mounds of a side, and which bear the seminal grooves, and a tumid median strip that bisects the depressed field contained within the former ridge-lines. The latter feature runs across mid-XVIII, and coalesces with the parenthetic ridges. The prostatic pores, in XVII and XIX, are coincident with the penial seta orifices, and are situated on sizeable porophore mounds. Genital markings a distorted ellipsoidal marking, median, in 16/17, consisting of a concavity with an irregular glandular centre (present in all specimens examined); small, rounded, blister-like markings present medially in the central concavities centred on 17/18 and 18/19: these may be single or paired (in which case they remain closely associated); the following combinations were observed: single markings at 16/17 and 18/19 (16.7% all specimens); single at 16/17, duplicated at 18/19 (14.3% all specimens); duplicated at 16/17, single at 18/19 (2.4% all specimens); duplicated at both 16/17 and 18/19 (66.7% all specimens). A further ellipsoidal depression with a similar blister-like centre (single or duplicated) is present at 19/20. A pair of shiny, blister-like markings also often visible in 17/18, in *ab*; similarly, a minute rounded pair of median glandular patches rarely encountered, between the prostatic pores of a segment. Female pores not always readily seen, due to clitellar tumescence, but when visible, appearing as small slits in *ab* (closer to *b*), midway between the setal arc and extreme anterior edge of XIV. Spermathecal pores 2 pairs of inconspicuous orifices in 7/8 and 8/9, aligned with *b* setae.

No septa strongly thickened/muscularised, though some in the forebody (especially 7/8–9/10) certainly appear to be slightly more robust than the remainder. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; these and the commissurals in XII are conspicuously larger than the remainder (which extend anterior to VI), and are the only latero-oesophageal commissurals,



**Fig. 69.** *Diploptrema quasifragilis* sp. nov., genital field of Holotype.

receiving delicate connectives from both the dorsal and supra-oesophageal vessels. The latter vessel untraceable. Gizzard fairly small, soft and lightly muscular, in V, with an expanded anterior rim. Oesophagus quite narrow, in VI–XVI, lacking calciferous glands or other elaborations; intestinal origin at 16/17, a definite dorsal typhlosole lacking. Nephridia simple, holonephric; the stomate, narrowly tubular bodies give rise to thin-walled ducts that enter the parietes close to *d* lines; anterior tufting absent. Holandric; 2 pairs of medium-large iridescent spermatic funnels and fine ?testicular material present in X and XI; 2 pairs of very large, coarsely loculate seminal vesicles in IX and XII, the latter masses somewhat



**Fig. 70.** *Diploptrema quasifragilis* sp. nov., right spermatheca of IX, Holotype.

the larger. Vasa deferentia not seen. Prostate glands 2 pairs of long, tortuous organs, the glandular portions of which are directed posteriad (the anterior pair extending to the environs of XXI–XXII, and anterior to XVI, the posterior set in XIX–XXIII, obviously smaller in overall size); prostatic ducts with a distinct muscular sheen, moderately long, winding, exiting to the exterior after passing through a 'glandular' mass lying under the nerve cord in XVII–XX; the latter, corresponding to the male field externally, is compartmentalised into regularly disposed white, cavitated sacs, the function of which is unknown. Copulatory musculature in this region is extensive; peniseta follicles fairly inconspicuous, with little attached musculature, the setae sparse, thin and fragile; the shaft, which is often twisted irregularly ectally, tapers gradually to a fine (often sharply recurved) tip; no ornamentation visible. Length of mature seta 1.50 mm; midshaft diameter 18.6  $\mu$ m (mean of 3). Ovaries, consisting of fan-shaped aggregations of oocytic strings, and small, translucent funnels present in XIII; a pair of distinct ovisacs present, adherent to the posterior face of septum 13/14. Spermathecae 2 subequal pairs, in VIII and IX; each comprises a subspheroidal ampulla, joined by a narrow isthmus to a short, blunt digitiform diverticulum, the inner walls of which are studded with numerous iridescent spermatic chambers; both the latter

spermathecal components share a very short duct. Length right spermatheca of IX 1.2 mm. Large genital seta follicles present in VIII, attached to the dorsal aspect of the body wall by a strong retractor ligament; setal glands absent. The setae few, fairly short; the ectal  $\frac{2}{5}$  of the shaft ornamented with widely spaced thorn-like spines that closely parallel the shaft for much of their length, curving outwards near their tips. Length of mature seta 0.59 mm; midshaft diameter 19.9  $\mu$ m (mean of 2).

### Remarks

As type specimens cannot be located, this species is erected on the illustration and account in Dyne (1984, unpublished) (ICZN 1999: Art. 73.1.4.).

*Diploptrema quasifragilis* belongs to the *D. fragilis* assemblage, members of which have the following morphological features: epilobous prostomium; nephropores in the vicinity of *cd*; slender body form; male pores slightly presetal, in XVIII; intersegmental markings restricted to the region XVI–XX; genital seta follicles strongly developed in VII, VIII or IX; penial setae fine and delicate, with little or no ornamentation; pharyngeal tufted nephridia absent; a large, glandular mass located under the ventral nerve-cord in the region XVII–XIX; spermathecae divided into a subspherical ampulla and a short, blunt, digitiform diverticulum bearing numerous sperm chambers on its inner surface (the spermathecae of *D. helonoma* are somewhat different from this).

*D. quasifragilis* may be readily identified in having seminal vesicles in IX and XII (thus differing from *D. fragilis*), long, sinuous prostate glands (the anterior pair extending at the least into XXI), a distinctive male field, and discrete ovisacs.

### *Diploptrema queenslandica* (Michaelsen, 1910)

(Fig. 71)

*Eodrilus queenslandicus* Michaelsen, 1910: 57–58, figs 1–3.

*Diploptrema queenslandica*; Jamieson and Dyne 1976: 450; Blakemore 1997: 1803–1804.

**TYPE LOCALITY:** Qld, 23°22'S 150°32'E, Rockhampton.

**TYPES:** HM V402 (re-examined).

**FURTHER RECORDS:** (Blakemore 1997) 23°26'S 150°27'E, Gracemere, 10 km SW of Rockhampton, ANIC RB.94.9.1.

**Description (after Michaelsen 1910; Jamieson and Dyne 1976)**

Length 120–185 mm. Width 4–5 mm. Segments ca 250. Proepilobous. Dorsal pores absent? Forebody triannulate, bulbous. Unpigmented white with dark dorsal line and yellow clitellum. Setae in regular rows throughout; ventral setal couples of XVIII present; those of XVII and XIX modified as penial setae; those of VII–IX modified as genital setae. Nephropores in *cd*. Clitellum in XIII–XIX; annular only in XIV–XV, in XIII, and XVI–XIX saddle shaped. Male pores in the setal arc, median of *a* lines, in XVIII. Genital markings absent. Prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices; seminal grooves distinct, convex laterally, skirting the *ab* setae of XVIII, and joining the porophores of a side. Female pores approximately aligned with *a* setae, midway between the setal arc of XIV and 13/14. Spermathecal pores in 7/8, 8/9, in *ab*.

Several septa in the vicinity of the anterior male system thickened (5/6–11/12 thickened, Blakemore 1997). Dorsal blood vessel in VII

towards the intestine double (Blakemore). Small lateral commissurals in VI–VIII, larger hearts in IX–XIII. Gizzard large, in V (Blakemore) or VI(?); oesophagus lacking calciferous glands. Intestinal origin from XIV–XVI, dilating to full width in XVII/XVIII (Blakemore); typhlosole not found. Holonephric; the stomate, avesciculate nephridial bodies with slender ducts, discharging anteriorly in their segments, in *cd*. Holandric; 2 pairs of racemose seminal vesicles in IX and XII. Ovaries in XIII. Prostate glands tubular, the anterior pair only slightly larger than the posterior set. Penial setae relatively delicate, generally with a simple bend; distally the shaft attenuates evenly, not clearly flattened; the distal  $\frac{1}{5}$  with distinctly pronounced ornamentation. The latter consists of transverse circlets of broad toothlets, generally in an alternating arrangement, but exhibiting considerable irregularity. Length of mature seta 1.75 mm; diameter 30  $\mu$ m. Large genital seta follicles with associated glands present in VII–IX. The setae, in general, fine; proximally rather strongly bent, simple distally; not particularly acute; the distal  $\frac{1}{4}$  ornamented with large, alternately disposed transverse groups of irregularly jagged teeth. Spermathecae 2 pairs, in VIII and IX, the posterior pair a little larger than the anterior set or equisized. Ampulla subspherical, the large, multiloculate diverticulum sessile, occupying the entire dorsal aspect of the duct; the duct slightly shorter than the diameter of the ampulla.

**Remarks**

The above description, taken in the most part from Michaelsen's (1910) original account, has been supplemented with brief notes made from a re-examination of the much-dissected type in the Hamburg Museum by Jamieson and from the account of new material by Blakemore (1997). Recognition of the gizzard location by the latter author as V rather than VI is probably correct. This species is characterised by the unusual ventral displacement of the male pores, and the presence of 3 pairs of genital setae (and distinctive associated glands), in VII–IX.

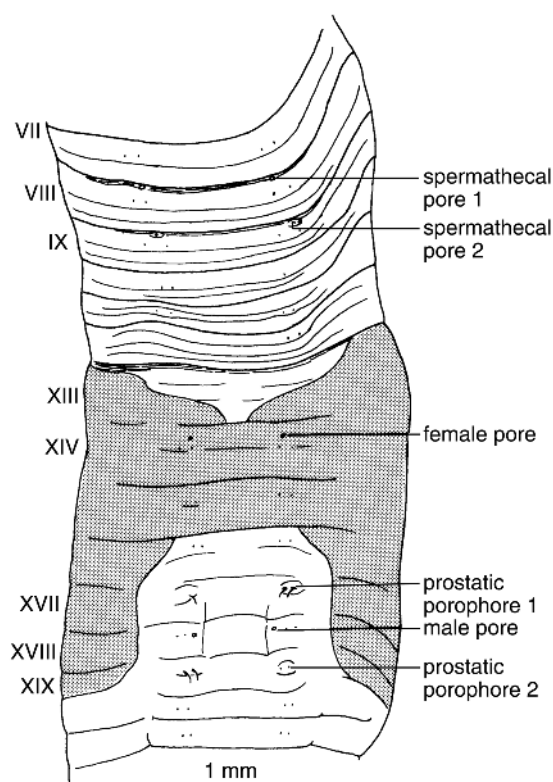
***Diploptrema rigida* sp. nov.**

(Figs 72, 73)

**TYPE LOCALITY:** QLD, 12°29'S 141°47'E, 32 km north of Weipa, along Pine Creek road, in leaf litter layer under dry, semi-deciduous vine forest. Coll. R. Raven, 6 Feb 1975.

**HOLOTYPE:** QMGH 2927.

**PARATYPES:** P1–3 QMGH 2928–2929.

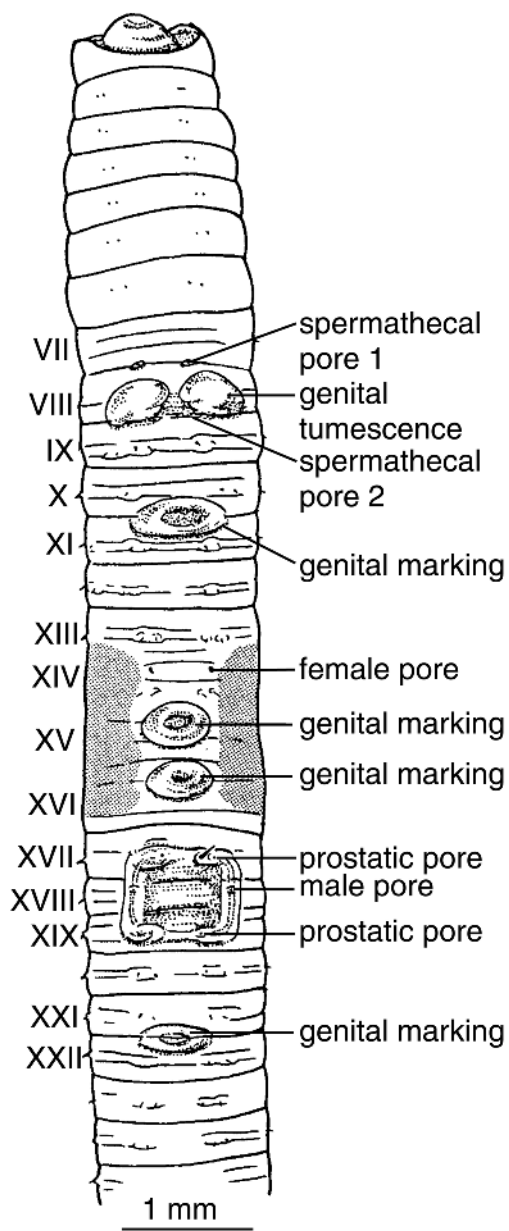


**Fig. 71.** *Diploptrema queenslandica* (Michaelsen, 1910), genital field of Syntype, HM V402, Original.

**Description**

Length 27, 31.5 mm. Width (midclitellar) 1.3, 1.2 mm. Segments 81, 98 (H, P1). Uniformly circular in cross-section throughout, pigmentless buff in alcohol, clitellum pale. Prostomium epilobous 1/2; first dorsal pore 12/13 (H), 11/12 (P1). Setae 8 per segment, in regular longitudinal rows throughout; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; those of VIII replaced by genital setae. Nephropores not externally recognisable. Clitellum saddle-shaped, strongly developed from slightly lateral of *b* lines continuously over the dorsal surface in  $\frac{1}{2}$ XIII– $\frac{1}{2}$ XVI (H),  $\frac{1}{2}$ III–XVII (P1); dorsal pores not obscured, intersegmental furrows faint. Male pores slightly lateral of *b* lines, just anterior of the setal arc, in XVIII; these are located in a pair of indistinct seminal grooves that join the prostatic porophores. The latter, in XVII and XIX, have distinct mounds, and coincide with the openings of the penisetal follicles. The seminal grooves lie in the middle of a slightly raised rim that circumscribes the male field. Genital markings paired tumescences associated with the presence of genital setae, are present in VIII; a series of unpaired, median genital markings, roughly elliptical in outline, and extending across *bb*, are present in 10/11, 14/15, 15/16 and 21/22 (in P1 and 3, all the above are present, with the exception of the marking in 15/16: P3 possesses markings at 10/11 and 21/22 only). Female pores are visible as minute points in *ab*, near the intersegment 13/14, in XIV. Spermathecal pores closely paired, slightly median of *a* lines, in 7/8 and 8/9.

No septa distinctly muscularised, though 7/8–8/9 appear to be very slightly thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; those in X–XIII sizeable, the remainder feeble; only the 4 posteriormost commissurals appear to be latero-oesophageal, receiving delicate connectives from both the dorsal and supra-oesophageal vessels, the remainder being dorsoventral only. Supra-oesophageal vessel evident from IX to XIII. Gizzard large and muscular, in V; oesophagus narrow, lacking pouching or calciferous glands, in VI–?XIV (intestinal origin not well defined, but probably in XV); a definite typhlosole lacking. Holonephric throughout, the stomate nephridial bodies discharging via avesculate, thin-walled ducts to the exterior in *cd*, closer to *d*; anterior tufting not demonstrable. Holandric; 2 pairs of large, brightly iridescent spermatic funnels — free in X and XI, both associated with adherent sperm masses. A single, large pair of sacciform seminal vesicles present in XII. Vasa deferentia obvious as iridescent tubes winding on the body wall, entering



**Fig. 72.** *Diploptrema rigida* sp. nov., Holotype, genital field.

the parietes in XVIII. Prostate glands 2 pairs of highly coiled, flattened-tubular structures extending into the vicinity of segment XXII. Penisetal follicles short, containing several reserve setae; the setae are slightly bent, their ectal ends somewhat

swollen, and with the margin in this region conspicuously inrolled to form a distinct cleft. Length of mature seta 0.77 mm; midshaft diameter 15.3  $\mu\text{m}$  (mean of 2). Ovaries and small funnels seen in XIII, ovisacs not detectable. Spermathecae 2 subequal pairs; each consisting of a sacciform ampulla fusing with a short, blunt, bipartite diverticulum, both portions sharing a short duct. Length of right spermatheca of IX = 0.97 mm. Fairly large genital seta follicles present in VIII, each containing a small number of small, straight setae; follicular glands absent. The setae ornamented over their ectal  $\frac{1}{2}$  with narrow, closely packed scalloping with acute edging. Length of mature seta 0.67 mm, midshaft diameter 18.6  $\mu\text{m}$  (mean of 2). In some specimens, the genital seta follicles are absent from VIII (?due to immaturity).

### Remarks

*Diploptrema* is represented on Cape York Peninsula by *D. ingrani*, and the diminutive *D. rigida*, both of which define the most northerly incursion of holonephric acanthodrilines currently recognised for Queensland. The habitats of the two species differ significantly: *D. rigida* is a litter species found in one of the small pockets of riverine vine-forest in the Weipa district, whereas *D. ingrani* has been collected from the drier open-forest community (dominated by *Eucalyptus tetrodonta*-*E. sp. aff. polycarpa*). The latter forest type is the most widespread community in Cape York Peninsula and holds promise of a rich earthworm fauna for the region, as yet largely unknown. The Weipa region is known to be a distributional overlap zone for the *Diploptrema* and *Neodiploptrema*. *D. rigida* may be distinguished

from other *Diploptrema* species by the combination of presence of genital setae, its distinctive genital field, the occurrence of only a single pair of seminal vesicles (in XII), and the unusual ectal cleft in the penial setae.

### *Diploptrema scheltingai* Jamieson, 1997

(Figs 74–76)

*Diploptrema scheltingai* Jamieson, 1997: 241–244, figs 9–11, 39.

**TYPE LOCALITY:** QLD, 13°44'17"S 143°20'15"E, Peach Creek, McIlwraith Range, altitude 500–520 m, in moist upper root horizon down to about 25 cm, notophyll vine forest with fan and feather palms, stream bank, sandy loam, on Kintore adamallite granite. Coll. K.R. McDonald, A.J. Stewart, 25–27 Sep 1996.

**HOLOTYPE:** QM G212001 (includes microscope slide of left genital seta of VIII).

**PARATYPES:** P1–2 QM G212003–212004; P3 QM G211981; P4 QM G213401; P5 QM G213406.

### Description (after Jamieson, 1997)

Length 74–104 mm. Width (midclitellar) 5 mm. Segments 188–204. Uniformly circular in cross-section throughout, pigmentless buff in ethanol, including clitellum. Prostomium prolobous but deeply indenting the peristomium dorsally; peristomium longer than segment II; first dorsal pore in 11/12 but not definitely perforate until 17/18. Setae 8 per segment, commencing on II; in XII, *aa: ab: bc: cd: dd* = 5.0: 1.0: 4.8: 1.0: 21.4; or 12.5: 2.5: 12.1: 2.4: 53.5%; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; setae *a* and *b* of VIII forming genital setae. Nephropores visible in the postclitellar body, a pair in each segment, each pore a faint spot anterior to each seta *b*. Clitellum well developed, extending over XII–XVII, interrupted ventrally by the male field in XVII, with doubtful midventral development anterior to the field, or interrupted between the ventral setal couples throughout, i.e. saddle-shaped. Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a minute oval papilla which is in line with the ventral setal couple (*ab*) of adjacent segments; the papillae of a side linked by a parenthetic seminal groove; the pore accompanied by one or more minute punctuations presumably representing penial setae, but the latter not protuberant; the posterior end of each seminal groove continuous onto a small transversely elliptical papilla which is centred lateral to *b* lines at the posterior limit of XIX; the male genital area depressed relative to the anteriorly bounding clitellum. Genital markings: a pair of rounded

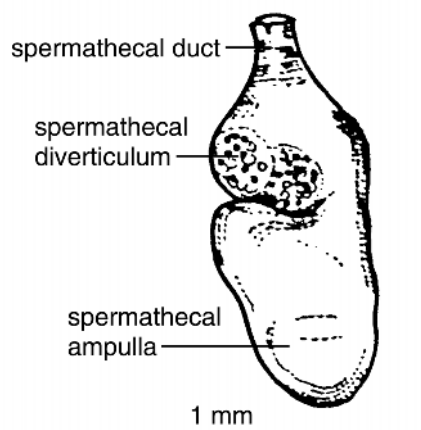
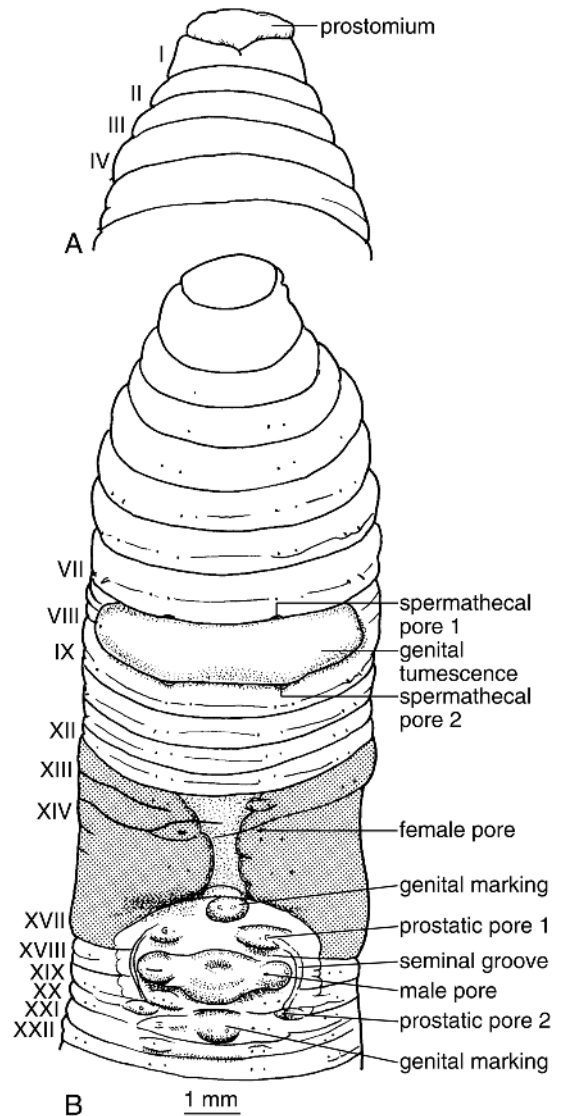


Fig. 73, *Diploptrema rigida* sp. nov., right spermatheca of IX, Paratype 1.

papillae in *ab* of XVIII, filling the segment longitudinally, the summit of each with a pore-like marking which from internal examination appear to be the male pore. The two papillae connected by a prominent transverse bar which is widened midventrally so as to impinge strongly on segments XVII and XIX, the widened region bearing a median elliptical protuberance. Further genital markings may include a small transversely elliptical pad anterior to the prostatic pores of XVII and a similar pad in XX with tumid lateral extensions which include the ventral setal couples. A strongly protuberant genital tumescence typically present in VIII fills, and expands the segment longitudinally, and takes in seta *c* on each side; genital setae present. Female pores a pair of small transverse slits, each with narrow border, presetally slightly lateral of *a* lines of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or very slightly lateral of setae *a*; inconspicuous but definite orifices, closely apposed to the genital tumescence.

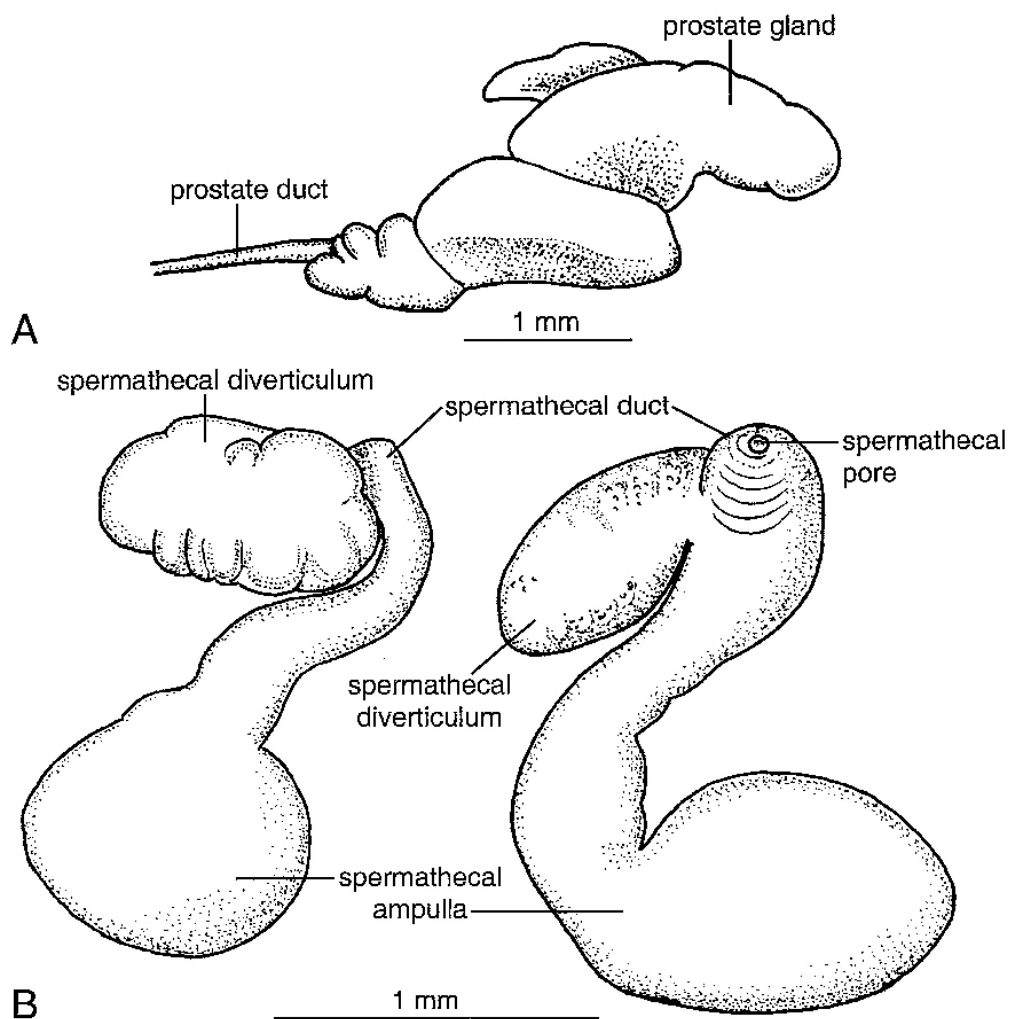
Septa 7/8–12/13 strongly thickened; 9/10–11/12 slightly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in X–XIII, latero-oesophageal, with connectives to the dorsal and supra-oesophageal vessels. Gizzard very large, an elongate, glossy, muscular, cylinder; in V. Oesophagus lacking calciferous glands; but very wide and vascular, without intersegmental constriction, in XVI and XVII. Intestine commencing, with abrupt expansion, in XX; a very large dorsal typhlosole commencing in XXII–XXIII, consisting of two distinct laminae. Holonephric, a large nephridium present on each side throughout but in caudal segments several longitudinal zigzagged ducts are present on each side running from one segment to the next; tufting absent. Holandric; testes, large sperm masses, and very large iridescent sperm funnels free in X and XI. Seminal vesicles racemose, in IX and XII; similar in size in the two segments. Small ovaries, with few egg strings, in XIII. Somewhat flattened tubulo-racemose prostates, two pairs, in XVII and XIX, restricted to these segments; those in XIX considerably larger than those in XVII, or the anterior pair slightly larger; each gland folded on itself at least twice, and, especially ectally, incised, so as to appear racemose; a narrow central lumen present but the surrounding glandular tissue very thick and its lobulation suggestive of lateral ductules; the external duct moderately long, and slender, medially directed, and accompanied by two large follicles of penial setae. The duct of each anterior prostate (examined closely in the holotype) discharges at a large bursa median to which is as



**Fig. 74.** *Diplotrema scheltingai* Jamieson, 1997: **A**, prostomium and first segments; **B**, genital field. [After Jamieson 1997]

smaller bursa associated with the penisetal follicles. The larger bursa overlies a more posteromedian smaller bursa, in XVIII, into which discharge the two thick, conjoined vasa deferentia of its side, these curving medially in a wide arc. The posterior prostate ducts do not appear to terminate at bursae but there are internal protrusions of the body wall near the point of entry of the penisetal follicles into the body wall. Penial setae curved through from 30° to 180°; the tip tapering to a smooth, simple point and bent to a





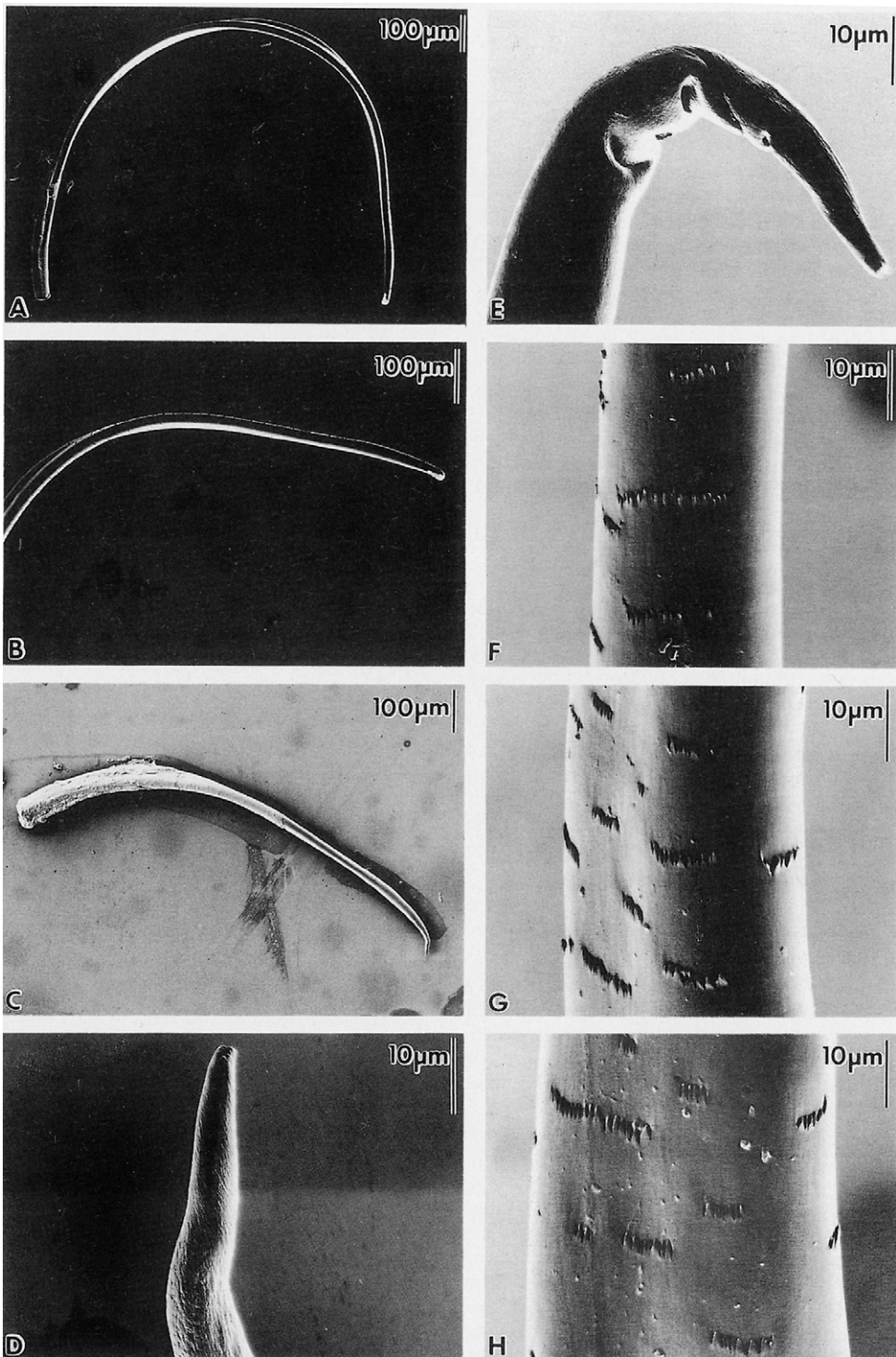
**Fig. 75.** *Diploptrema scheltingai* Jamieson, 1997, Holotype: **A**, right prostate *in situ*; **B**, right posterior spermatheca in dorsal and ventral view. [After Jamieson 1997]

varying extent; sculpturing consisting of many unevenly spaced groups each of several contiguous pointed teeth; near the tips the groups are extensive circumferentially at fairly regular longitudinal intervals of approximately 1.7  $\mu\text{m}$ . Genital setae, in VIII, gently curved but a short basal region more strongly curved in the same direction; more slender relative to length than usual for *Diploptrema* but with the usual longitudinal notching and expansion of the tip below the terminal point; length (straightened) = 1.8 mm; greatest width, near base, = 51  $\mu\text{m}$ . Spermathecae 2 pairs, in VIII, and IX, the posterior pair slightly the larger; each with an

ovoid ampulla and longer, slender fairly well demarcated duct which is joined near its swollen ectal end by a large, ellipsoidal, multiloculate diverticulum containing many minute iridescent balls of sperm; length left spermatheca of VIII = 2.6 mm; length ampulla = 1.1 mm; ratio length spermatheca: length duct = 1.7; greatest dimension of diverticulum = 0.9 mm.

#### Remarks

The tripartite transverse bar on segment XVIII is distinctive of *D. scheltingai*. The fact that the nephridia, though apparently only one pair per segment (preservation being inadequate for certain determination of their condition), have multiple



**Fig. 76.** *Diploptrema scheltingai* Jamieson, 1997, Holotype, scanning electron micrographs: A-C, two right penial setae of XIX; D, tip of C; E-H, appearance of seta shown in A and B from the tip to near the base. [From Jamieson 1997]

longitudinal ducts possibly merits placement of this species in *Neodiploptrema*. The validity of separating *Neodiploptrema* from *Diploptrema* is uncertain as there is evidence that the meronephric condition of the latter taxon has evolved more than once from the holonephric *Diploptrema* condition. If so, recognition of the Ocotchaetinae or Octochaetidae, already refuted from molecular studies (Jamieson *et al.* 2002) (e.g. Fig. 3) and on cladistic grounds would be further undermined (see also Remarks under Acanthodrilinae and *Neodiploptrema*).

### ***Diploptrema schmardae* (Beddard, 1892)**

*Acanthodrilus schmardae* Beddard, 1892: 132.

*Notiodrilus schmardae*; Michaelsen 1900b: 137.

?*Eodrilus daemeli* Michaelsen, 1910: 58–60.

?*Diploptrema daemeli*; Jamieson and Dyne 1976: 450.

**TYPE LOCALITY:** Qld, near Rockhampton, in freshwater.

**TYPES:** Unknown.

#### **Description (after Beddard 1892; Jamieson and Dyne 1976)**

Length 60 mm. Width 5 mm. Dorsal pores absent. Setae paired. Clitellum saddle-shaped, XII–XVII (or XIII–XVIII?). Genital setae in VIII and IX.

Five thickened septa behind the gizzard. Prostates coiled; the anterior larger than the posterior pair. Genital setae with setal glands in the vicinity of the spermathecae; smaller than the penial setae, differing in form and unornamented. Penial setae curved, at the distal end transversely swollen. Posterior spermathecae larger than the anterior pair; with a small knoblike diverticulum at the distal end. Spermathecal diverticulum multi-loculate, occupying the whole dorsal aspect of the duct, but smaller than the ampulla.

#### **Remarks**

*D. schmardae* should probably be regarded as a *species dubium* as the description appears inadequate for identification. It is possibly the synonym of *D. daemeli* and if this were confirmed it would constitute the senior synonym as it has chronological priority.

### ***Diploptrema spectabilis* sp. nov.**

(Figs 77, 78)

**TYPE LOCALITY:** QLD, ca 19°31'S 147°8'E, banks of Crooked Gully Waterhole, 1.6 km. from Giru, under tall grass in sandy alluvium. Coll. G. Dyne, 10 Feb 1975.

**TYPES:** The number of specimens is not specified by Dyne (1984). Fragmentary material observed by BGMJ, with this locality, is cited in the ANIC catalogue as GD.95.30.1.

#### **Description**

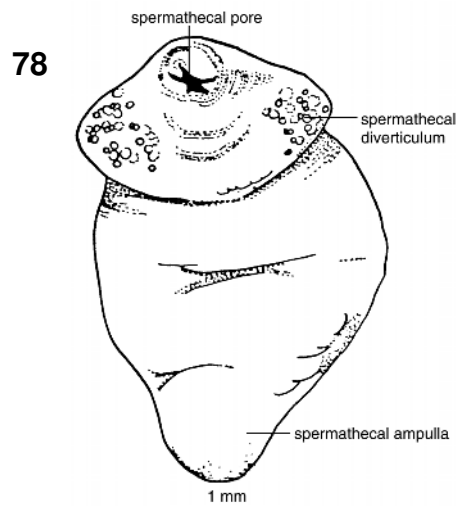
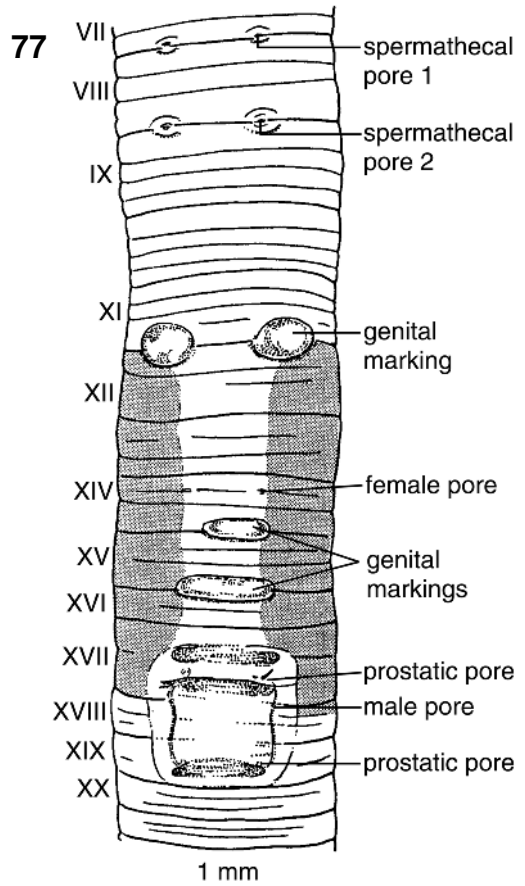
Length 343 mm. Width 9.1 mm. Segment numbers not determinable. Form uniformly circular in cross-section; colour whitish-grey in alcohol, pinkish-white in life. Prostomium prolobous; first dorsal pore at 11/12. Setae 8 per segment commencing in II, in regular rows throughout; setae in XVII and XIX modified as enlarged penial setae, genital setae lacking. Most somatic setae small and not readily detectable; ventral setal couples retained on XVIII. Nephropores prominent in the clitellar region, in a single series, slightly dorsal of *d* lines. Clitellum well developed, though unpigmented, saddle-shaped, extending over segments XII–XXII, dorsal pores and setae visible, segmentation obscured dorsally. Male pores small, visible in faint seminal grooves, lateral of *b* lines, virtually in intersegment 17/18. Two pairs of combined prostatic and penial setae orifices in XVII and XIX, the anterior pair on a ridge emphasised by depressions immediately anteriad and posteriad; the posterior pair are not raised, but lie in front of a very shallow depression in XIX. Genital markings a prominent pair of ventrolateral papilliform swellings in 11/12 (all specimens); unpaired tumid bands ventrally, in 14/15 and 15/16, the latter marking slightly more elongate, and extending across *bb*. Female pores barely pre-setal, in *b* lines, in XIV. Spermathecal pores 2 pairs, the posterior orifices the more conspicuous, protruding slightly atop broad, conical tumescences.

Septa 5/6 moderately thick; 6/7–11/12 strongly muscularised and thickened; (8/9–9/10 possibly the strongest) 12/13 weakly muscularised, the remainder thin. Dorsal blood vessel inter-segmentally bifurcate anteriad of XVIII (rejoining at the septa), but remaining single anteriad of VI. Last hearts in XIII, those in XI–XIII with equisized connectives from both the dorsal and 'supra-oesophageal' network, remainder dorso-ventral only. The supra-oesophageal component appears to consist of dorsal blood plexi restricted to segments X–XIV, but not apparently interconnected. Gizzard very large, dolioform and muscular, in V. Oesophagus fairly broad, undifferentiated, though rather vascular in XII–XV. Intestine commences in XVII, a low dorsal typhlosole present after about XXX. Ingesta: soil mixed with organic debris, including grass stalks and wood fragments. Holonephric nephridia avascular, with conspicuous nephrostomes in *ab*, and thin-walled ducts entering the parietes in

*d* lines. No anterior tufting demonstrable, but definite enlargement of the nephridial bodies detected. ?Holandric; 2 small pairs of rather diaphanous, non-iridescent spermathecal funnels in X and XI; 2 pairs of large seminal vesicle masses present in IX and XII; the posterior spermathecal funnels are conspicuously larger. The anterior portion of the male system is heavily infested with small, whitish cysts, possibly of Protozoan origin. Prostate glands 2 unequal pairs, in XVII and XIX, the anterior set very much larger than the posterior pair. Each organ is restricted to its segment of origin, and consists of a much flattened, tubular glandular portion which is deeply incised, and a muscular, fairly tightly coiled duct that is somewhat dilated at its extreme ectal end, as it enters the body wall musculature. Associated with the ducts are conjoined penisal follicles, containing at least 6 reddish penial setae (undescribed). Ovaries consisting of long, diaphanous, germinative tissue invested in the same peritoneum as the nephridial bodies, confined to XIII; few oocytes detected (?spent); unusually long, vertically oriented oviducal funnels also seen in XIII; ovisacs absent. Spermathecae of unequal size, those in IX considerably larger than the pair in VIII. Each organ comprises a flask-like ampulla, and small, ledge-like diverticulum sessile on the ventral aspect of the point of fusion of the ampulla and the short duct. Length right spermatheca of IX 3.6 mm.

### Remarks

*Diploptrema spectabilis* bears a striking resemblance to *D. pseudospectabilis*, and, as discussed in the remarks covering that species, appears to be undergoing a transition to the microscolecin condition. More detailed sampling may reveal that *D. spectabilis* and *D. pseudospectabilis* represent populations of the same, highly variable species, but for the present, there are sufficient anatomical differences to justify retention of specific status for the 2 entities. Points of similarity between these congeners are as follows: prominent tubercular genital markings in 11/12, male pores in 17/18, dorsal blood vessel bifurcate in the oesophageal region, low dorsal typhlosole present, nephropores in *d* lines, compact spermathecae with completely sessile diverticulum. *D. spectabilis* differs in having retained (albeit vestigially) the posterior and anterior sets of prostate glands and spermathecae respectively, and in lacking any vascular outpouchings in the oesophageal region.



**Figs 77, 78.** *Diploptrema spectabilis* sp. nov., Holotype. 77, genital field; 78, right spermatheca of IX.

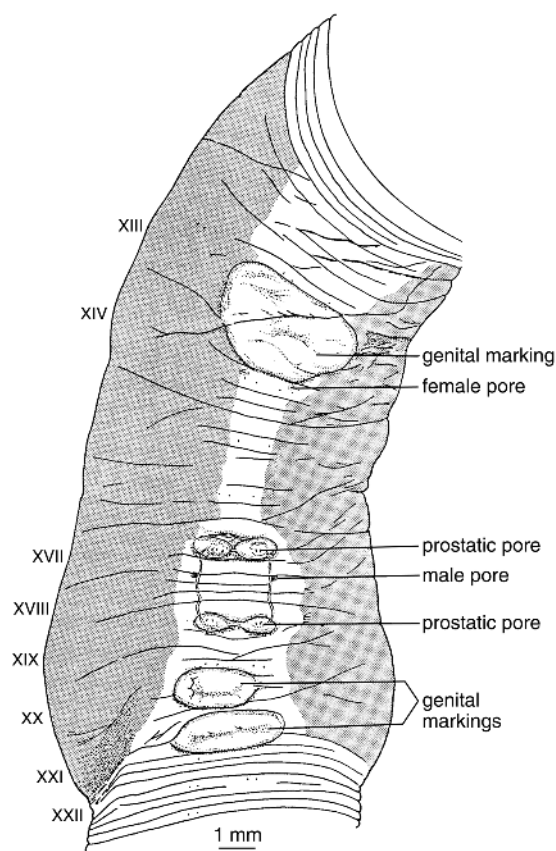
***Diploptrema spenceri* sp. nov.**

(Figs 79, 80)

**TYPE LOCALITY:** QLD, Upper Endeavour River.**HOLOTYPE:** a single specimen from the W. Baldwin Spencer collection of the National Museum of Victoria, labelled: 'Upper Endeavour River, July, 1898 NMVG 491'; this specimen is not listed in Jenzs and Smith (1969).**Description**

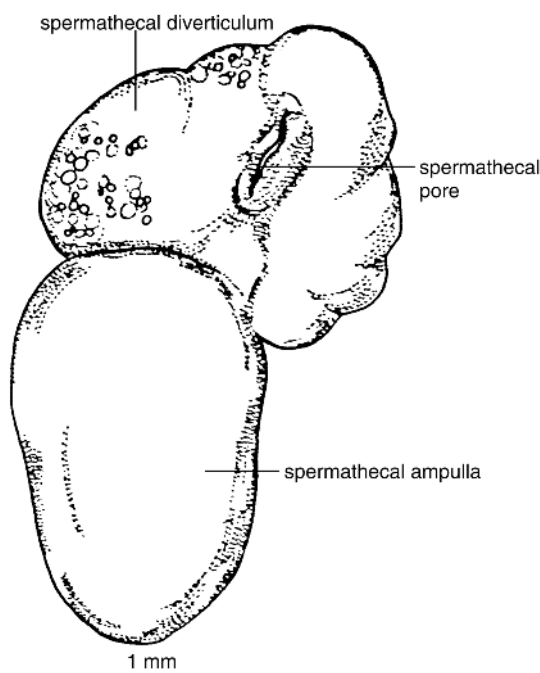
Length 300+ mm (posterior amputee). Width (midclitellar) 8.8 mm. Segments ? Form circular in cross-section throughout, the body tapering noticeably from the anterior to posterior ends. Prostomium probolous; first dorsal pore not demonstrable, presumed to lie within the clitellar region. Setae 8 per segment, in regular rows throughout, not always easy to detect in the extreme forebody and hindbody; ventral setal couples of XVIII absent; ventral setal couples of XVII and XIX modified as penial setae; genital setae lacking. Nephropores not detectable externally. Clitellum saddle-shaped, tumid, extensive over XII–XXI, more strongly developed dorsally; intersegmental furrows and setae visible, dorsal pores obscured. Male pores a pair of conspicuous slits on small, rounded papillae, situated far anteriad in XVIII (just posterior to 17/18), well lateral of *b* lines, and slightly lateral of the narrow, well-defined seminal grooves joining the prostatic porophores of a side in a roughly straight line. The prostatic pores, coincident with the penial seta orifices, are located on low mounds that appear to form part of the general tumescence circumscribing the male field. Genital markings a large, flattened, disc-like tumescence centred medially on 13/14, and extending longitudinally from between the setal arc of XIII to the intersegment immediately anteriad of the setal arc in XIV, and laterally well beyond *b* lines; 2 smaller, flattened, median ellipsoidal markings are present in 20/21 and 21/22, the posterior tumescence the larger. Female pores a small pair of presetal orifices in XIV, just above *b* lines. Spermathecal pores 2 pairs of obvious, simple openings aligned with *ab*, in 7/8 and 8/9.

Septa 5/6 unthickened, 6/7–11/12 with strong muscularisation, 12/13 slightly thickened, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, these and the commissurals in XII very large, and receiving connectives from both the dorsal and supra-oesophageal vessels (the latter seen in XII–XVI only); commissurals in X and XI large, but not latero-oesophageal; remainder still considerable, dorsoventral only, and diminishing in size anteriad. Gizzard very large, shiny and



**Fig. 79.** *Diploptrema spenceri* sp. nov., genital field of Holotype.

incompressible, in V; oesophagus fairly wide, vascular, in VI–XVII; a single pair of stalked calciferous glands, extending from XV to XVII; these are internally lamellate, highly vascular, and, with intersegmental constrictions, give the superficial appearance of several pairs, though all chambers are continuous, and only a single stalk to the oesophagus is demonstrable, in XVI. Intestine commences in XVIII, a very prominent typhlosome commences in XX, attaining maximal size by XXV; this consists of a thickened strip of tissue running along the dorsal aspect of the intestine (beneath the dorsal vessel); the typhlosome is bisected by a deep mid-dorsal cleft, the two portions also having lateral aliform extensions. Holonephric; stomate, elongate nephridial bodies throughout, their avascular ducts entering the parietes at somewhat variable distances above, though commonly approximately  $\frac{3}{4}$  *bc* dorsal of *d*; extensive tufting present anteriorly: large masses of astomate loops definitely demonstrated for III–V, their thick, composite ducts not traced, but



**Fig. 80.** *Diplotrema spenceri* sp. nov., right spermatheca of VIII, Holotype.

presumed to end in the buccal cavity; the bodies in IV by far the largest, consisting of hundreds of small component loops. Holandric; 2 pairs of large, complexly folded and iridescent spermathecal funnels present in X and XI; 2 pairs of very extensive, finely loculated seminal vesicle masses in XI and XII; vasa deferentia prominent as pairs of closely associated, thickened ducts adherent to the body wall on each side of the oesophagus, becoming single, much dilated muscular ducts in XVIII, prior to entering the parietes. Prostate glands 2 pairs of comparatively simple, loosely coiled tubular organs, opening to the exterior at XVII and XIX through short, muscular ducts. Closely associated are 4 pairs of short, opaque penisetae attached to the glandular portion of the prostates by mesentery, and to the body wall by retractor ligaments. The setae taper gradually, the shaft often with a simple bend ectally, the ectal  $\frac{1}{8}$  with low transverse rows of irregularly jagged teeth; these are difficult to detect due to their small size and proximity to the shaft, resulting in a faint, striated appearance to the seta under moderate magnification; the rows become discontinuous entally, breaking up into small, scattered clusters. Length mature seta = 3.14 mm; midshaft diameter = 46.6  $\mu$ m (mean of 3). Small bundles of oocytes, and large, plicate funnels present in XIII, ovisacs

absent. Spermathecae 2 subequal pairs, both sets in VIII, the anterior seta opening to 7/8, the posterior to 8/9; each consists of a flask-shaped or roughly tubular ampulla, which merges with a broad, flattened, roughly semicircular diverticulum which occupies the entire dorsal aspect of the very short duct; the diverticula are packed with numerous, iridescent internal chambers that appear to be arranged in a bipartite manner. Length right spermatheca of 8/9 = 3.1 mm (base of ampulla to pore). Genital seta follicles lacking.

#### Remarks

*Diplotrema spenceri* is unique in exhibiting the following combination of characteristics: absence of genital setae, male pores close to 17/18, calciferous glands, and extensive anterior nephridial tufting. Many more closely related species undoubtedly remain to be discovered, particularly in the moist forests between the Endeavour and Bloomfield Rivers; until such time as collections are forthcoming from this region, *D. spenceri* remains morphologically and geographically isolated from the remainder of the genus.

#### *Diplotrema sulcata* sp. nov.

(Figs 81, 82)

**TYPE LOCALITY:** QLD, 20°17'S 148°17'E, Conway Range National Park, approximately 200 metres up main walking track, in damp black soil and mud near an estuarine swamp. Coll. G. Dyne and A. Postle, 14 Jun 1974.

**HOLOTYPE:** QMGH 2898.

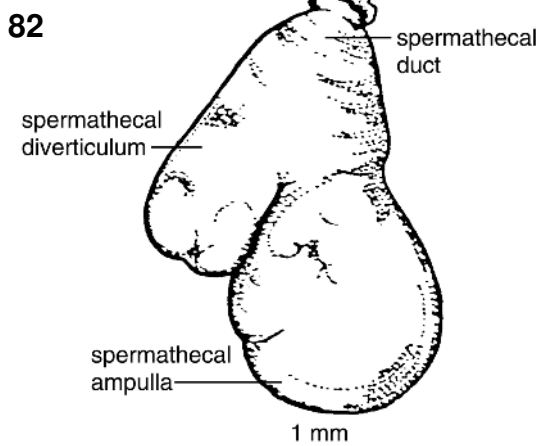
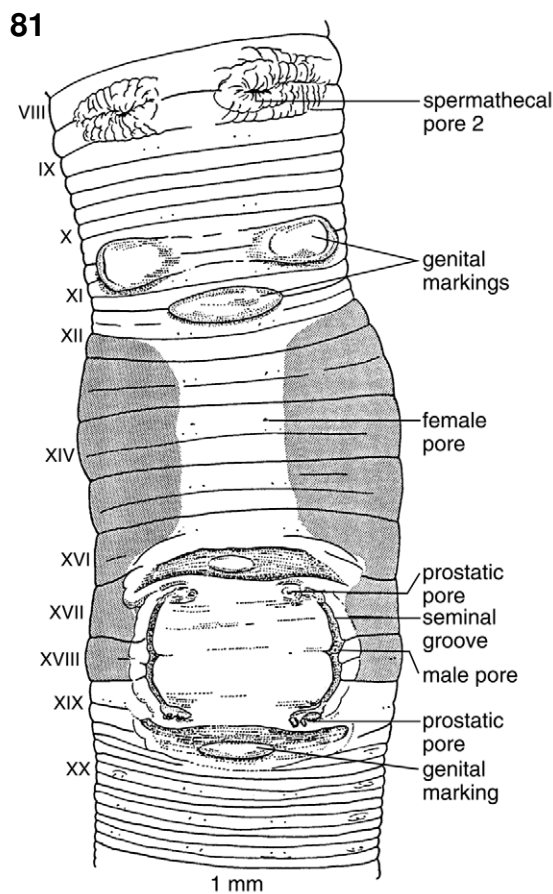
**PARATYPE:** QMGH 2899.

#### Description

Length 42+, 27.5+ mm (posterior amputees). Width 4.0, 4.1 mm. Segments ? (H, P1). Uniformly circular in cross-section throughout, grey-white in alcohol, clitellum faintly pigmented. Prostomium prolobous, first dorsal pore 10/11. Setae 8 per segment, commencing on II; ventral setal couples absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital seta modifications lacking. Nephropores visible as faint, whitish points on the clitellum (intersegmentally), slightly irregular in disposition, approximately mid-way between *d* lines and the mid-dorsal line. Clitellum tumid, saddle-shaped over the posterior half of XII to XVII; dorsal pores occluded, intersegmental furrows and setae still visible. Male pores readily seen at the bottom of deep seminal grooves that resemble fissures, and which connect the prostatic porophores of a side. The male pores are closer to intersegment 17/18 than the equatorial line of XVIII, and are situated

well lateral of *b* lines. The central portion of the male field is a well-defined, raised quadrangle, with slight median concavities, delimited laterally by the seminal grooves, and anteriorly and posteriorly by long-ellipsoidal depressions centred on 16/17 and 19/20. The latter concavities have small, rounded markings located medially within them. The prostatic pores, in XVII and XIX, define the four corners of the male region; these openings are quite discrete from the exit points of the penial setae, being lateral to the latter. Genital markings a pair of rounded, elliptical tumescences extending across *ac* are present in 10/11; a single median marking is located in 11/12 (across *bb*) — both specimens. Female pores inconspicuous slits, located presetally, in XIV, in *a* lines. Spermathecal pores 2 pairs, on shortly conical papillae that are elaborately furrowed and puckered, in 7/8 and 8/9, aligned with *b* setae.

Septa 5/6 thin, 6/7 slightly thickened, 7/8–9/10 moderately muscularised, remainder delicate. Dorsal blood vessel single; last hearts in XIII; commissurals in XI–XIII seen to receive connectives from both the dorsal and supra-oesophageal vessels; whether the commissural in X is similarly latero-oesophageal not determinable. Gizzard cylindrical: large and muscular, in V, with a soft anterior proventriculus; oesophagus is suppressed, and the septa deflected by the gizzard to segment X. Oesophagus fairly wide, reaching maximal expansion in XIII, pouching calciferous glands lacking. Intestine begins in ?XVI (in P1 commencing in XVII), lacking a definite typhlosole. Holonephric; conspicuous funnels seen in *ab*, the nephridial bodies extending past *d* by a distance approximating *ad*; the thin ducts were seen to enter the parietes well above *d* lines, just short of the midpoint between *d* and the mid-dorsal line; anterior tufting absent. Holandric; 2 pairs of large brightly iridescent spermatic funnels and coagulated ?sperm masses present in X and XI; 2 pairs of seminal vesicle masses, consisting of large component loculi, attached to the posterior faces of septa 10/11 and 11/12. Prostate glands 2 pairs of flattened, tortuous tubular organs, their muscular ducts straight and of moderate length, entering the body wall in XVII and XIX. The anterior prostates extend into segment XV anteriorly, and into XX posteriorly, and are noticeably larger than the posterior pair, which extend posteriorly to XXI. The associated penisetal follicles are inserted in the body wall a short distance from the terminal ends of the prostatic ducts; the follicles have separate *a* and *b* components, and are well-supplied with copulatory musculature (as is the general area of the male



**Figs 81, 82, *Diploptrema sulcata* sp. nov., Holotype. 81, genital field; 82, right spermatheca of VIII.**

field). The penial setae are relatively broad, and flattened, with a pale yellowish sheen; much of the shaft is smooth, only the distal densely clothed with fine, ectally directed spinules that appear to be arranged in discrete clusters. Length of mature seta 2.57 mm; midshaft diameter 103  $\mu$ m (mean of 2). Ovaries, consisting of very small oocytic clusters, and large oviducal funnels, seen in XIII, ovisacs not discernible. Spermathecae 2 subequal pairs in VII and VIII, discharging posteriorly in their segments, each with an ovoid ampulla, and short, blunt, sacciform diverticulum; both these components fuse to give a dilated chamber below the short, muscular duct. Length of right spermatheca of VIII 2.3 mm; insemination of the diverticulum indicates biparental reproduction. Genital seta follicles absent.

### Remarks

*Diploptrema sulcata* is sympatric with *D. conwayi* and *D. tenuiseta*, though not clearly related to either. It is easily recognised by the conspicuous, deeply furrowed seminal grooves, the lack of genital setae or nephridial tufting, and the abrupt attenuation of the penial setae.

### *Diploptrema tenuiseta* sp. nov.

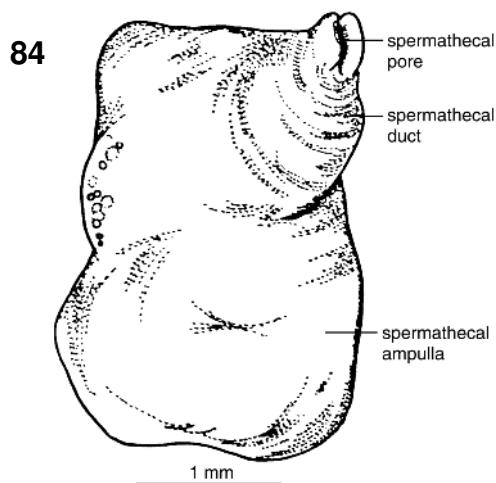
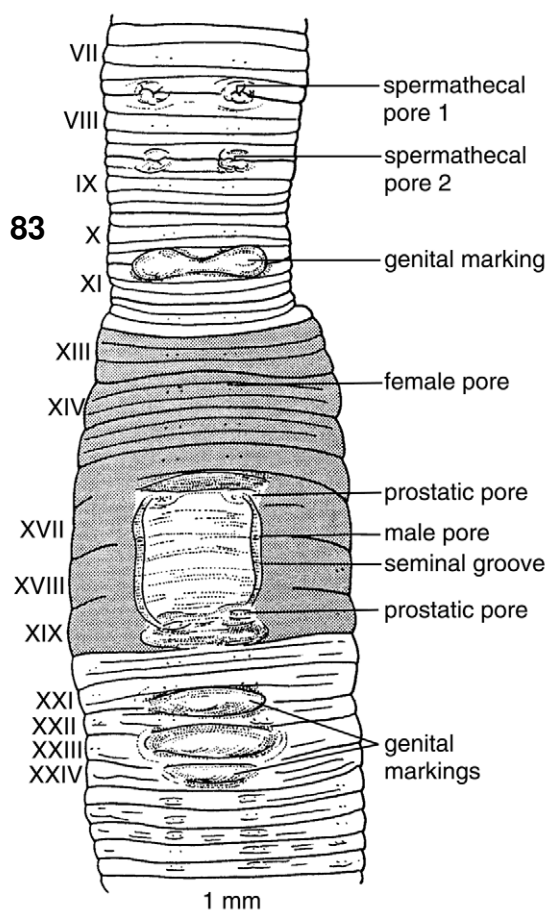
(Figs 83, 84)

**TYPE LOCALITY:** QLD, 20°17'S 148°46'E, Conway Range National Park, approximately 200 m up the main walking track in damp black soil and mud near an estuarine swamp. Coll. G. Dyne and A. Postle, 14 Jun 1975.

**HOLOTYPE:** QMGH 2891.

### Description

Length 210. Width (midclitellar) 11.8 mm. Segments 271. Form circular in cross-section throughout, grey-buff in alcohol, clitellum grey. Prostomium prolobous, first dorsal pore 11/12. Setae 8 per segment, the ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; genital setae lacking. Nephropores cannot be distinguished externally. Clitellum well developed, annular, extending over segments XIII–XIX; dorsal pores obscured, intersegmental furrows still obvious. Male pores a pair of minute orifices, virtually in 17/18, lateral of *b* lines, located in broad, though shallow, seminal grooves linking the prostatic porophores of a side. The prostatic pores are confluent with the penial seta openings, on slight mounds, in XVII and XIX; the anterior pair lie on a raised strip, in sharp relief to a distinct, long-elliptical concavity antieriad. The entire male field (as confined between the seminal grooves) is a pigmentless rectangle, its 4 corners occupied by the prostatic porophores, and surrounded laterally by clitellar tumescence.



**Figs 83, 84, *Diploptrema tenuiseta* sp. nov., Holotype. 83, genital field; 84, right spermatheca of IX.**



Genital markings a median, bipartite tumescence extends from mid-*bc* to mid-*cb* in 10/11; a pair of well-defined, intersegmental pads with tumid surrounds lie in 21/22 and 22/23, with a similar smaller marking in 23/24. Female pores seen presetally in an intra-segmental groove, approximately in *a* lines (slightly shifted towards *b*), on XIV. Spermathecal pores on conspicuously protuberant and furrowed papillae, in 7/8 and 8/9.

Septa 5/6–10/11 strongly thickened with muscular bands; (5/6, 9/10–10/11 somewhat weaker than the remainder), 11/12 slightly thickened, other septa delicate. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; the commissurals in X–XIII are much larger than the remaining vessels, and are demonstrably latero-oesophageal; supra-oesophageal vessel strongly developed, seen in X–XIV. Gizzard large, cylindrical, thickly muscular, in V, directing septa up to and including 9/10 posteriad. Oesophagus moniliform, fairly short, lacking pouching or calciferous glands; intestinal origin at XVIII. Holonephric; a single pair of elongate nephridial bodies per segment, their large, preseptal nephrostomes obvious in *ab*; the avesiculate ducts are somewhat variable with regard to their point of discharge to the exterior, but this is always well above *d* lines; anterior tufting absent. Holandric; 2 pairs of large, convoluted and iridescent

spermatic funnels present in X and XI; 2 pairs of large, acinous seminal vesicles in XI and XII. Two pairs of flattened, tortuous prostate glands restricted to XVII and XIX, the anterior pair obviously the larger; the ducts are shiny and muscular, though narrow, with single loops. Prominent penisetal follicles are intimately associated with the latter; these are ligamented to the body wall just short of the mid-dorsal line. The setae are long, fine, and fragile, ornamented over the ectal region with ?continuous circlets of fine teeth. Length of mature seta 7.20 mm; midshaft diameter 33.5  $\mu$ m (mean of 3). Ovaries not seen, but a large pair of oviducal funnels are present in XIII, close to the nerve-cord. Spermathecae sac-like, approximately equisized, in VIII and IX, each consisting of a large, irregular ampulla (bent ectally to form a short, tapering, muscularised duct), and a 'diverticulum' that is almost completely embedded in the ampulla, manifested externally only by a slight out-pouching and feeble iridescence. Length right spermatheca of IX 3.3 mm. Genital seta follicles absent.

#### Remarks

*D. tenuiseta* may be distinguished from its congeners by the following combination of characteristics: genital setae and anterior nephridial tufting absent, seminal vesicles in XI and XII, penial setae long and fine.

MICROSCOLECIN QUEENSLAND *DIPLOPTREMA* SPECIES*Diploptrema glandifera* (Jamieson, 1995)

New combination

(Figs 85–89)

*Rhododrilus glandifera* Jamieson, 1995: 575–578, figs 1, 2A–C, 3A–F.

**TYPE LOCALITY:** QLD, 17°35'S 145°45'E, altitude 400–440 m, Palmerston National Park, along track to Nandrooya Falls. Coll. K. McDonald, J. Ledger, D. Ledger, Sept 1994.

**HOLOTYPE:** QMG211465.

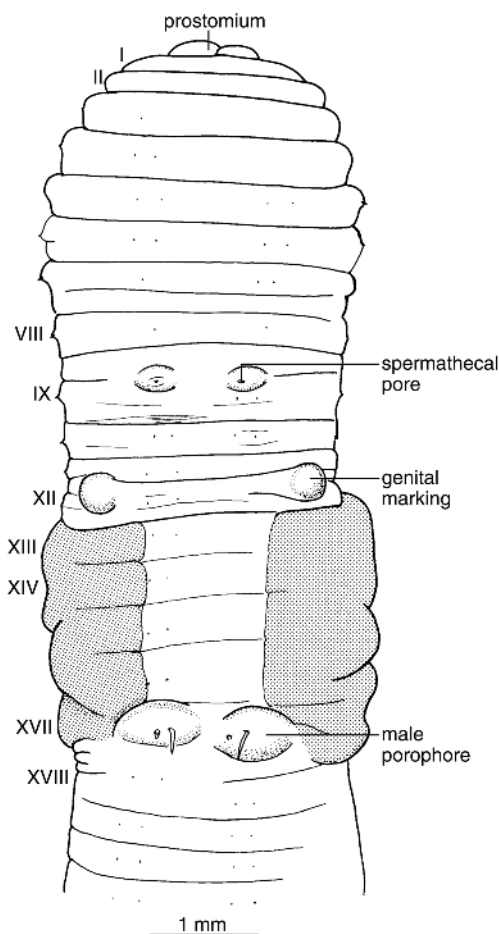
**PARATYPE:** QMG211478 (P1); QMG211511 (P2; includes slide of anterior end).

**FURTHER MATERIAL (Dyne 1984):** (1) QLD, 17°32'S 146°01'E Palmerston National Park, in red volcanic soil under complex mesophyll vine-forest, 40 km from Innisfail. Coll. G. Dyne, 9 Feb 1975, QMGH 2924. (2) same locality. Coll. G. Dyne, July 1975: 2 clitellates, 2925, also ANIC GD.95.68.2. (3) Qld, 17°37'S 145°50'E, Wallacha Falls, Palmerston National Park. Coll. T. Walker, 26 May 1972: a single clitellate, QMGH 2926.

**Description (after Jamieson, 1995)**

Length 58 mm. Width, midclitellum, 3.2 mm. Segments 195. Colour pigmentless in ethanol. Prostomium not determinable. First dorsal pore 9/10. Setae lumbricin, closely paired; the pairs widely separated; in XXVIII:  $aa: ab: bc: cd: dd = 4.7: 1: 4.7: 1.4: 17$ ; or  $13.0: 2.8: 13: 3.7: 47.5\%$ . Clitellum in XIII–XVII, strongly tumid, saddle-shaped with ventral margins shortly lateral of *b* lines. A pair of combined male and prostatic pores in XVII, on indistinct oval porophores, each pore directly behind two strongly protuberant penial setae; a pair of tubular prostates visible through the body wall, winding from XVII to XXIX. Genital markings: a pair of distinct papillae in inter-segmental furrow 11/12, in *bc*. Female pores? (see Further material). Spermathecal pores a single pair, in intersegmental furrow 8/9, in *ab* lines, on conspicuous papillae which extend into VIII and IX.

Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII. Gizzard large, strongly muscular, in V; preceded by a wide proventriculus which is not constricted off from it. Calciferous glands in each of the six segments X–XV there is a conspicuous pair of large, white, nacreous elongate sacs that curve upwards from the ventrolateral aspect of the oesophagus which they invest on each side to its dorsal aspect; each with longitudinal plications in its proximal half; the glands are not effervescent in acid alcohol.



**Fig. 85.** *Diploptrema glandifera* (Jamieson, 1995), genital field of Holotype. [After Jamieson 1995]

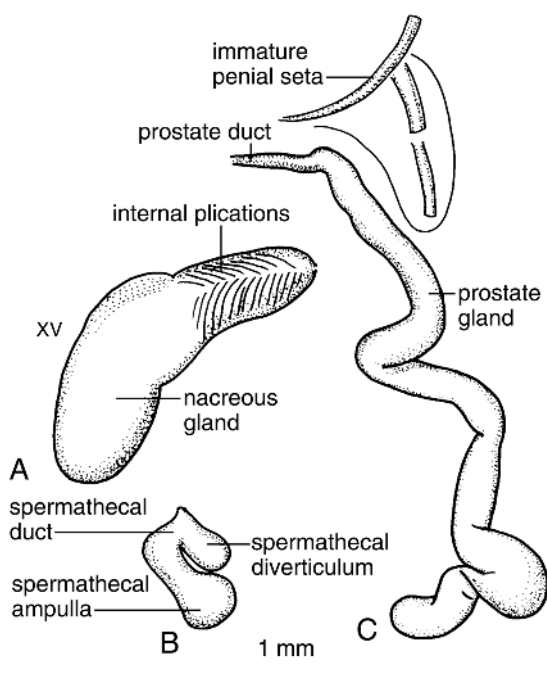
Intestinal origin XVI. Typhlosole not observable. Nephridia avascular holonephridia. Iridescent sperm funnels in X and XI; racemose seminal vesicles in IX and XII. Ovaries, with large oocytes, in XIII. Prostates a single pair, long tortuous and slenderly tubular; each with a slender, poorly demarcated duct. Penial setae present, two to four projecting at each male porophore; the setae strongly curved, through at least 90°; with a pointed tip; the ectal region of the shaft with numerous palmate ectally directed scales, closely applied to the surface; length of a seta 1.9 mm, measured around the curvature, or 1.3 mm in a straight line from base to tip. Spermathecae 1 pair, discharging anteriorly in IX; with an ovoid or somewhat clubbed ampulla and a broadly

digitiform diverticulum almost as long (left) or about half the length (right), converging at the pore without intervention of an appreciable duct.

**Further material** (QMGH 2924–2926, Dyne 1984, unpublished)

Length 41–53 mm. Width (midclitellar) 2.7–2.9 mm. Segments 177–199. Prostomium pro-epilobous; first dorsal pore 8/9 (one segment further forward than types). Penial setae in XVII, ornamentation (seen in the types of *glandifera*) not detected. Nephropores usually visible on the clitellum in the intersegments, in *d* lines. Clitellum saddle-shaped, XIII–XVII, partially encroaching into XVIII ventrally. Combined male and prostatic pores on conspicuous papillae in XVII, coincident with the penial seta orifices; setae often protruding. The papillae occasionally conjoined by a median ridge and extending laterally well into *bc*. Genital markings a pair of large, transversely pyriform, domed tumescences extending between *a* and distance *ab* beyond *b*, in 18/19, a peripheral concentric furrow demarcating a central portion of each papilla (constant); a similar pair of markings in 19/20 in some (not seen in types of *glandifera*); a further pair in 11/12, extending laterally to mid-*bc* (constant). Female pores minute, seen presetally, in XIV, a little lateral of *b* lines. Spermathecal pores a single pair, in 8/9, with slightly protuberant lips, in *ab*.

Septa 5/6–9/10 with some musculature, 7/8 the thickest (not strongly developed, however). Dorsal blood vessel single; last hearts in XIII, those in XII and XIII conspicuously larger than the remainder, and receiving thin connectives from both the dorsal and supra-oesophageal vessels; commissurals in X–XI possibly with similar connections, remaining vessels definitely dorsoventral only; supra-oesophageal vessel seen in X–XII, its exact limits not determinable. Gizzard moderately large, globular, in V; oesophagus short, in VI–XVI, very large thin-walled diverticula present in X–XIII (not X–XV, unlike types of *glandifera*). Intestine commencing in XVII (not XVI), a very strong dorsal typhlosome present after approx. segment XXII (not seen in types of *glandifera*). Nephridia with avesculate ducts seen entering the parietes consistently in *d* lines; no anterior tufting demonstrable, though the pre-intestinal nephridia are usually larger and more complexly coiled. Holandric; 2 pairs of large, iridescent spermathecal funnels, apparently enclosed in delicate laterally directed testis-sacs (sacs not seen in *glandifera* types); seminal vesicle-like masses in XI and XII; IX with a definite pair of seminal vesicles. Vasa deferentia faint, winding tortuously on the body wall, entering the parietes independent of the prostatic duct (approximated with the latter at the



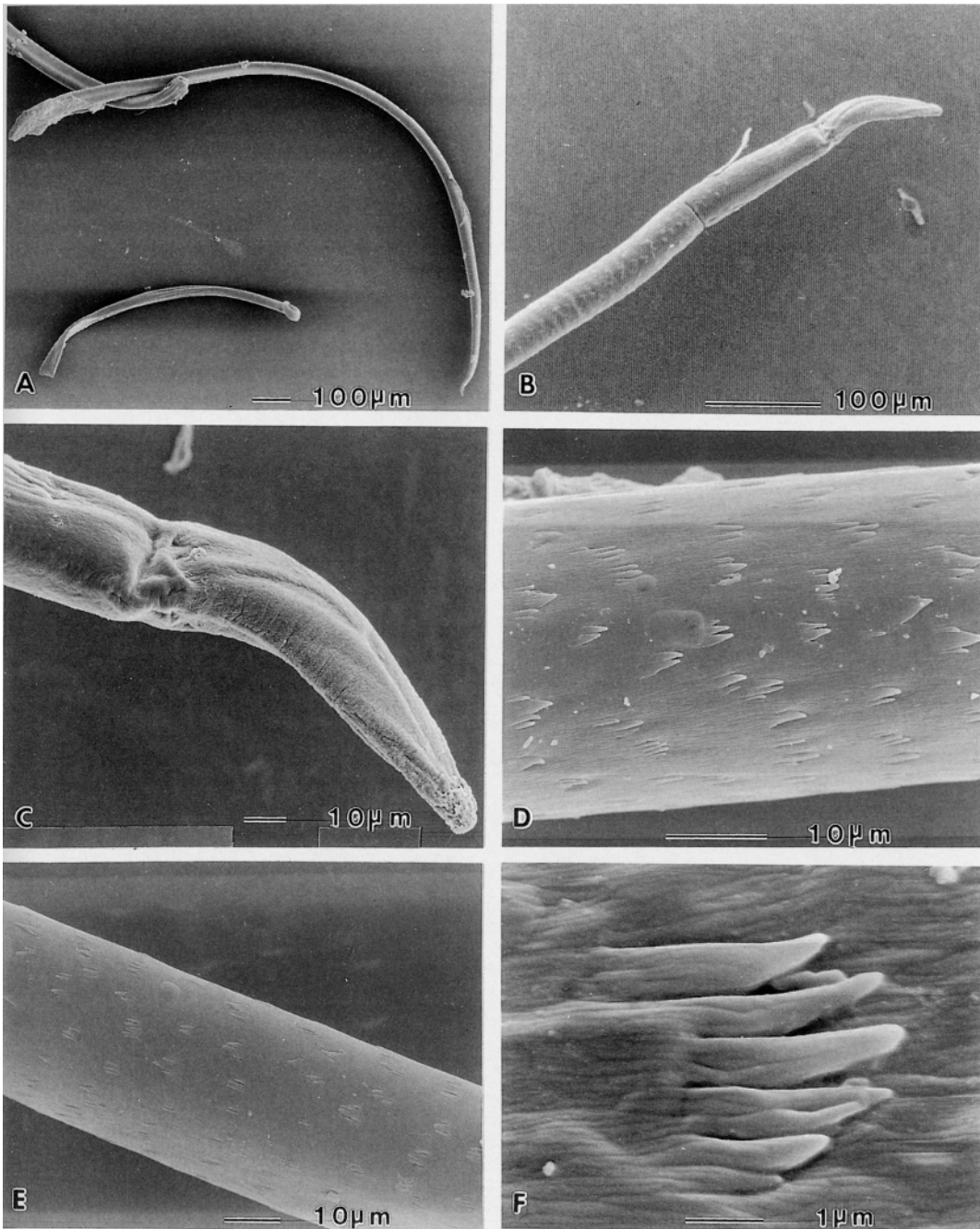
**Fig. 86.** *Diploptrema glandifera* (Jamieson, 1995). Paratype QMG211478: **A**, a nacreous gland of XV; **B**, right spermatheca; **C**, right prostate gland.

[After Jamieson 1995]

pore?); prostate glands a pair of coiled, flattened, tubular structures, may extend posteriorly to XXII or XXV, or anteriorly; the short muscular duct enters the parietes through the *b* seta orifice. Penial seta follicles well developed, strongly curving, following the glandular portion of the prostates, *a* and *b* follicles clearly distinguishable; extending posteriorly as far as XXIII (P1). The setae bending strongly only near the ectal end; the tip clearly flattened, spathose; no ornamentation present on the shaft; length of mature seta 3.05 mm; midshaft diameter 62.1  $\mu$ m (mean of 3). Small ovaries and funnels seen in XIII. Spermathecae a single pair, in IX, each organ consisting of a sacciform ampulla bent at its junction with the somewhat fan-shaped diverticulum; the latter contains numerous small, spheroidal, iridescent flecks on its inner walls; duct of moderate length. Length right spermatheca of IX = 1.7 mm (apex of ampulla to pore).

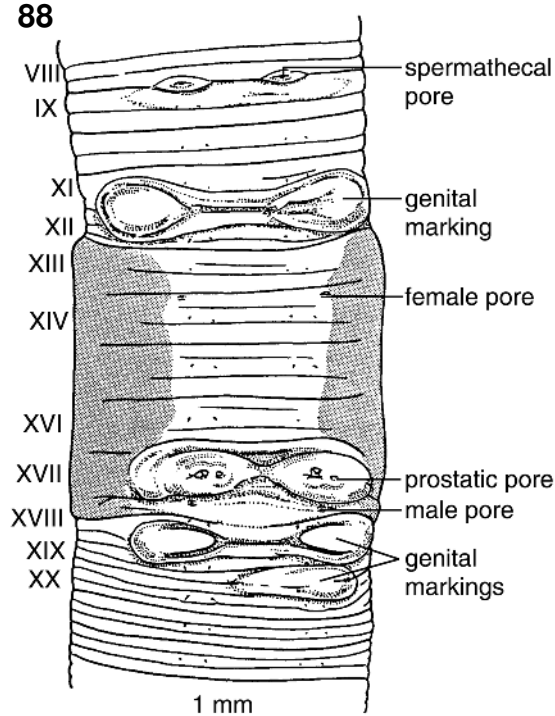
#### Remarks

*Rhododrilus glandifera* Jamieson, 1995, is here transferred to the microscolecin portion of *Diploptrema*. A study of its mitochondrial DNA sequences shows it to lie within *Diploptrema* (Jamieson 2000; Jamieson *et al.* 2002: fig. 3).

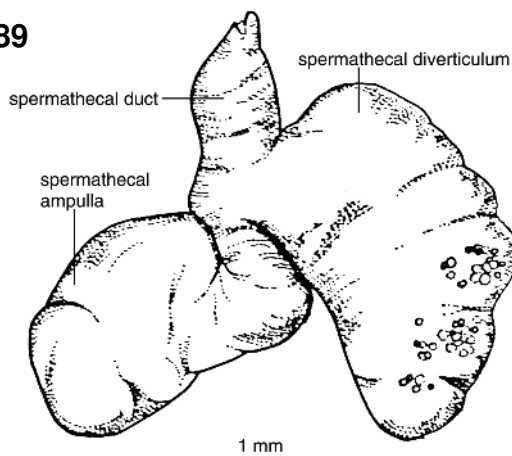


**Fig. 87.** *Diplotrema glandifera* (Jamieson, 1995), Paratype, scanning electron micrographs of penial setae: **A**, whole seta; **B**, ectal end; **C**, ectal tip; **D**, **E**, scale-like sculpturing of ectal region; **F**, detail of a scale.  
[From Jamieson 1995]

88



89



**Figs 88, 89.** *Diploptrema glandifera* (Jamieson, 1995), QMGH 2924. **88**, genital field; **89**, left spermatheca of IX.

*Rhododrilus glandifera* was described by Jamieson (1995), in response to a request for identification of material supplied by Mr Keith McDonald. It now appears that material described as a new, microscolecin species of *Diploptrema* ('*D. palmerstoni*') by Dyne (1984, unpublished) belongs to the same species. The large conjoined genital papillae in 11/12, the single pair of spermathecal pores, on protuberant papillae, in

ab of 8/9, and the saddle-shaped clitellum in XIII–XVII, are notable similarities. Some pertinent parts of Dyne's description (1984, unpublished) are given under Further material, above; it has not been incorporated in the above account but is illustrated.

This species was one of the three microscolecin species included within *Diploptrema* by Dyne (1984, unpublished) because of obvious affinities with geographically proximate acanthodrilin forms. The correctness of this decision is borne out by the 12S mtDNA data.

The closest acanthodrilin species to *D. glandifera* is *D. athertoni*, with which it shares the following features: broadly flattened (or at least spatulate) penial setae, digitiform oesophageal diverticula, similar spermathecal construction, and nephropores in the vicinity of *cd*. An ancestral form, linking both species in the past, is envisaged; fixation of the microscolecin condition in an isolated population would have rendered impossible or restricted any further gene flow between the latter and the acanthodrilin forms. Within the microscolecin section of *Diploptrema*, *D. glandifera* may be diagnosed from its unique genital field and the possession of gut diverticula.

### *Diploptrema pseudospectabilis* sp. nov.

(Figs 90, 91)

**TYPE LOCALITY:** QLD, 19°23'S 146°57'E, Alligator Creek, approximately 3 km from the entrance to Mt Elliot National Park, in dry creek bank. Coll. G. Dyne, 10 Feb 1975.

**HOLOTYPE:** ANIC GD.95.10.1.

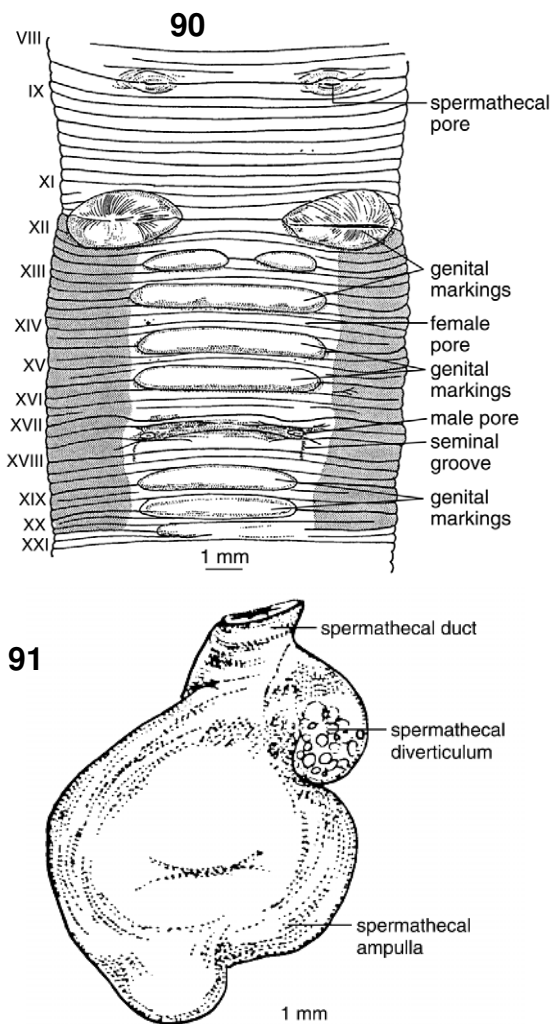
**PARATYPES:** P1 and 2 ANIC GD.95.10.1.

### Description

Length 230 mm. Width (midclitellar) 9.2 mm. Segments 365. Form circular in cross-section, pigmentless buff in alcohol; clitellum, where developed, a purplish-grey. Prostomium prolobous, peristomium with conspicuous longitudinal furrowing. First dorsal pore in 11/12. Setae 8 per segment, commencing in II, generally small and difficult to discern; ventral setal couples of XVIII present; those of XVII modified as penial setae; genital setae lacking. Nephropores barely visible externally, as faint points in the intersegmental furrows, just dorsal of *d* lines. Clitellum faintly developed, saddle-shaped, more distinct dorsally, extending from XII–XX [from drawing] (tumid, and well developed in the 2 paratypes). Male pores obscured by segmental overlap, but when exposed, appear as distinct, rounded orifices, lateral of *b* lines, in 17/18, in very faint seminal grooves; the latter extend from

the prostatic pores to a point in the anterior part of XVIII, where they end blindly. Prostatic pores a pair of openings just median of tiny papillae, in mid-XVII; these are located in a transverse depression running across *bb*, which is overhung by torose brows both anteriorly and posteriorly. Genital markings a large pair of tubercular swellings laterally situated (*b* to mid *bc*) in 11/12, with a central crease (intersegmental furrow); a series of long, intersegmental tumid pads across *bb*, approximately half a segment in breadth: small, paired, in 12/13, with larger, single markings present in 13/14, 14/15 and 15/16; a slightly smaller, and less distinct series present in 18/19, 19/20 and 20/21 (the latter faint and only partially developed). Female pores tiny slits in *ab*, on slightly ?glandular areas on XIV. Spermathecal pores a single pair, in 8/9, on prominently swollen lips, aligned with *ab*.

Septa 5/6 slightly thickened, 6/7 moderately so; 7/8–10/11 much thickened, and reinforced with bands of musculature; 11/12 only moderately affected. Dorsal blood vessel single posterior to XVIII; anterior of this segment, with regular segmental bifurcation, rejoining at each intersegment; the final bifurcation present in VI, thereafter single, and continuous onto the pharynx. Last hearts in XIII, though those of XII are the larger; only the latter 2 commissurals receive connectives from both the dorsal and supra-oesophageal vessels; the latter was detected in XII–XV only. Gizzard very large, muscular and incompressible, in V; oesophagus narrow, highly vascular, internally rugose, expanded into vascular outpouchings in XIII and XIV (and to a slight degree in XII), which communicate freely with the oesophageal lumen. Intestine commences in XVIII, a low, dorsal typhlosole commencing at XXIX–XXX. Nephridia simple, stomate holonephridia with large, elongate nephrostomes and wide, conspicuous ducts that enter the parietes in *d* lines, all in a single series on each side. No tufting present in the pharyngeal region, though the nephridial bodies are somewhat enlarged. Holandric; 2 pairs of small to medium-sized spermathecal funnels that are much folded but only slightly iridescent, in X and XI; 2 pairs of loosely compacted, racemose seminal vesicle masses in IX and XII, the posterior pair conspicuously the larger. Both the funnels and the seminal vesicles are infected by masses of whitish cysts, possibly of protozoan origin. Vasa deferentia seen as faintly iridescent tubes, which plunge into the thick body wall musculature in XIII, and are thereafter not traceable. A single pair of tightly coiled, compact, tubular organs in XVII, the ducts fairly long, and muscular, also compactly tortuous. Small,



**Figs 90, 91.** *Diplotrema pseudospectabilis* sp. nov., Holotype. **90**, genital field; **91**, right spermatheca of IX, lateral view.

inconspicuous penisal follicles are associated with the ducts, and contain a small number of rather short, reddish setae. Copulatory musculature in the male field region strongly developed (thick ligaments joining the ventral and dorsal aspects of the body wall), but little musculature associated with the penisal follicles. The penial setae short, fairly straight, the ectal  $\frac{1}{3}$ – $\frac{1}{4}$  of the shaft ornamented with staggered, incomplete circlets of jagged teeth; length of mature seta 2.17 mm; midshaft diameter 40.4  $\mu$ m (mean of 2). Ovaries a single wafer of oocytic strings, together with large funnels, in XIII, ovisacs absent. Spermathecae a single pair, in IX, consisting of a bulbous, ovoid ampulla (rather irregular in outline), and a sessile,

indiscrete, inseminated diverticulum; both share a very short, muscular duct, that arises from their junction. Length right spermatheca of IX 2.9 mm.

### Remarks

*Diploptrema pseudospectabilis* has a single pair of prostatic pores, with the male pores separate, in 17/18. This particular arrangement is common among New Zealand species of the genus *Rhododrilus*, and, as is the case in *D. pseudospectabilis* clearly represents an intermediate degree of organisation between the acanthodrilin and microcolecin facies. This species is of considerable interest, because an acanthodrilin species having a morphology that could well be considered immediately ancestral to that exhibited by *D. pseudospectabilis* was discovered nearby. This was *D. spectabilis*, a form that is clearly related to the latter species, even to the extent of having an intrasegmentally bifurcate dorsal vessel and large, tubercular genital markings in 11/12. In *D. spectabilis*, there is a second pair of prostate glands and spermathecae, but these are considerably smaller than the anterior and posterior sets of organs respectively; their complete elimination would result in an anatomy very similar to that of *D. pseudospectabilis*. Such forms provide a valuable insight into the mechanisms by which variations in the genital system may become fixed, and hence, their relative importance in higher classification. It may be added that this example suggests that the microcolecin condition has been acquired more than once in *Diploptrema*.

### *Diploptrema retractata* sp. nov.

(Figs 92, 93)

**TYPE LOCALITY:** (1) QLD, 16°05'S 145°28'E: Cape Tribulation, NQ, in moist rainforest soil (complex mesophyll vine-forest). Coll. W. Nash and J. Nash, 15–19 Aug 1975.

**PARATYPE LOCALITIES:** (1) As above, 7 clitellates, 2 semi-mature specimens (P1–9). (2) same locality. Coll. W. Nash and M. Shand, to Jan 1975, 1 clitellate (P10), fragments.

**HOLOTYPE:** (1) Lodgement?

**PARATYPES:** (1) Paratypes 1–9; (2) Paratype 10, lodgement?

### Description

Length 85, 115 mm. Width (midclitellar) 3.1, 3.8 mm. Segments 202, 228 (H, P1). Body uniformly circular in cross-section throughout, a pale whitish-grey in alcohol, clitellum a pale pink. Prostomium pro-epilobous; first dorsal pore 10/11 (H, P1). Setae in regular rows throughout, commencing in II, intersetal distance *cd* wide

(> 2*ab*); ventral setal couples of XVII modified as greatly enlarged penial setae; those of IX replaced by genital setae. Nephropores visible as pigmented points on the clitellum, approximately aligned with *d*-setae in the intersegments. Clitellum tumid, annular, over XIII–XVII; dorsal pores occluded, intersegmental furrows and setae distinct. Combined male and prostatic pores a pair of distinct orifices at the anterior ends of a pair of distinct seminal grooves, located in mid-XVII (post-setally) in *ab*, closer to *a*. A single, obvious slit slightly anterior and median to the combined male pores represents the exit point of the penial setae. The conspicuous feature of the male field is the presence of fairly wide, deep, and sharply defined seminal grooves, which run from the combined pores posteriad, ending blindly at the anterior edge of XVIII. Genital markings a series of paired, intersegmental tumescences present in 18/19–21/22, each set consisting of conjoined elliptical markings with concentric, glandular centres, confined within *bb*. Paratype variation: P1 — postclitellar markings lacking; P2 — 20/21 right side only; P3 — markings in 18/19 (and left. side in 19/20) lacking; P4 — additional elliptical, midventral markings present in 14/15, 15/16; P5 — postclitellar markings absent; P6 — markings present in 19/20, 20/21, and right. side of 20/21 only; P7 — markings in 19/20–21/22 and an additional one in 15/16 present. Female pores located presetally in XIV, in *ab*. Spermathecal pores a single pair with puckered rims, in 8/9.

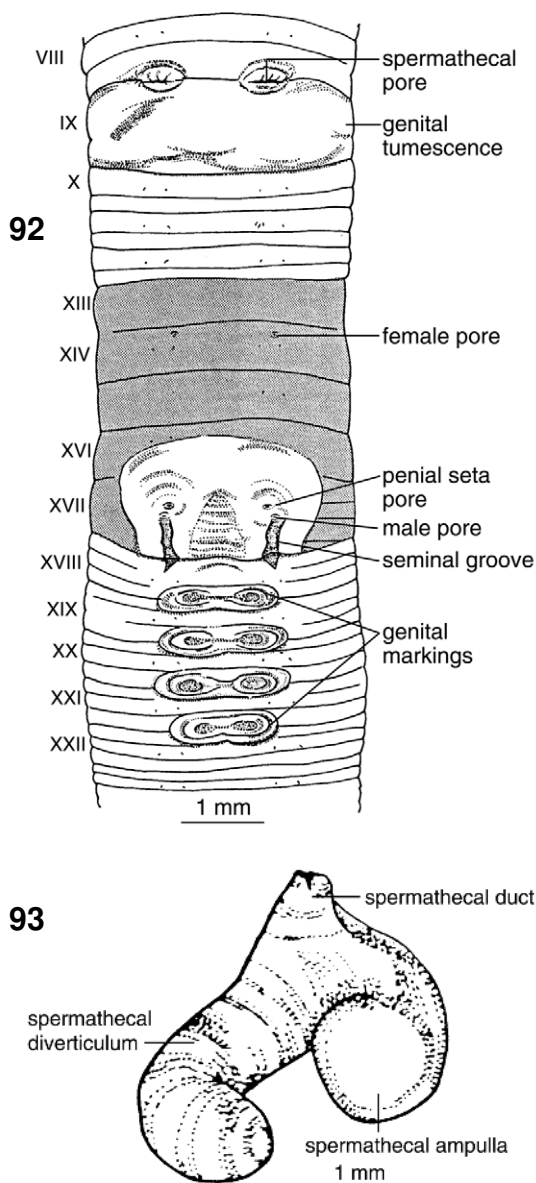
Septa 6/7 thin, 7/8 slightly thickened, 8/9–11/12 moderately muscularised, remainder diaphanous. Dorsal blood vessel single, traversing the gizzard to the pharynx; last hearts in XIII; only these and the commissurals in XII are sufficiently large to be termed 'hearts', though the vessels in X and XI are also latero-oesophageal. Remaining commissurals dorsoventral only; supra-oesophageal vessel detected in X–XIV. Gizzard fairly large, compressed dorso-ventrally, but firm and muscular, in V. Oesophagus moniliform, well-vascularised, in VI–XVI; paired, lamellate, dorso-lateral calciferous glands present in XIV–XV (occasionally also in XIII). Intestine commences abruptly in XVII, a low, dorsal typhlosome present after XXVI. Holonephric; stomate, avesiculate nephridial bodies confined to the body wall between setal lines *a* and *d*; the thin-walled ducts were observed to enter the body wall close to *d* lines. Anterior tufted nephridia lacking, though the nephridial bodies in segments II–IV are very much enlarged. Holandric; 2 pairs of large, convoluted funnels present in X and XI, with extensive, finely loculate seminal vesicles in IX and XII, flecked with spermatozoal iridescence.

Vasa deferentia seen embedded in the body wall anterior to XVII, thence visible as 2 distinct tubes on each side, which enter a glandular mass in XVII, close to the point of exit of the prostatic duct; the two ducts presumably fuse at or near the pore. Prostate glands a single pair of very extensive organs consisting of a sinuous system of flattened coils that extend anteriorly to XV, and posteriorly to the vicinity of XXI; the ducts are shiny and muscular, looping once before dilating ectally, as they enter the glandular region in XVII. Penis setal follicles very large, in the form of diaphanous sheets covering a large portion of the dorsal aspect of the prostates (*in situ*); within the follicles are a number of large setae, the shafts of which are strongly bent; the follicles are ligamented to the body wall by protractors (attached ventrally), and retractors (attached near the mid-dorsal line). The setae exit via orifices anterior to that of the combined male pores, in XVII. The shaft of each seta is somewhat flattened, tapering to a dull point, and lacking any ornamentation. Length of mature seta 3.74 mm; midshaft diameter = 80.5  $\mu\text{m}$  (mean of 3). Sheaves of oocytes and small funnels present in XIII. Spermathecae a single pair, in IX, consisting of a small, spheroidal ampulla, and a fairly long, digitiform diverticulum which bears brightly iridescent spermathecal chambers on its inner ental wall; a short isthmus connects the latter two components, and above this point of fusion, arises a short duct. Length right spermatheca (base of diverticulum to pore) = 2.3 mm. A pair of large genital seta follicles present in IX; no obvious glands present; the setae rather straight, the ectal  $2/5$  ornamented with compact scalloping having prominent, striated overhangs; these are sparsely arranged over the shaft, becoming denser towards the tip. Length of mature seta 1.45 mm; midshaft diameter 34.2  $\mu\text{m}$  (mean of 2).

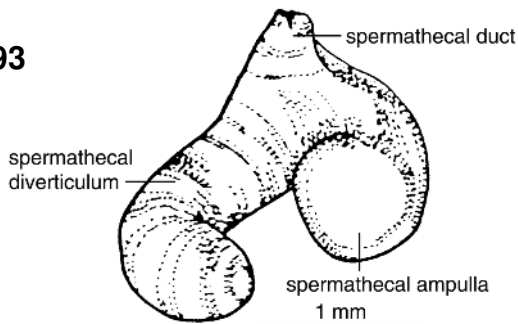
### Remarks

As type specimens cannot be located, this species is erected on the illustration and account in Dyne (1984, unpublished) (ICZN 1999: Art. 73.1.4.).

As noted by Dyne (1984, unpublished), advanced microscolecin reduction is a feature of *Diploptrema retractata*; the male and prostatic pores are approximated on XVII, but with a distinctive, though functionless (?) seminal groove leading posteriad to XVIII. It appears to have no close relatives, and is restricted to the Cape Tribulation area. Subsequent collections, not available at the time of description, confirm that the microscolecin condition is a consistent feature. The species favours lowland habitats: on an altitudinal transect between Cape Tribulation and Mt Pieter-Botte (1070 metres), *D. retractata* was not recovered



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**Figs 92, 93, *Diploptrema retractata* sp. nov., Holotype.**  
92, genital field; 93, right spermatheca of IX.

from collecting sites at altitudes exceeding 300 metres. Further peculiarities of the species include the presence of definite dorso-lateral calciferous glands in the region XIII–XV, large, strongly bent penial setae and associated musculature, and spermathecae differing markedly in structure from the usual *Diploptrema* form (having a long, tubular diverticulum).



NEW SOUTH WALES *DIPLOPTREMA* SPECIES\*

\*One Queensland subspecies is included here.

*Diploptrema tyagarah* Dyne, 1979b

*Diploptrema tyagarah* Dyne, 1979b: 38–41, fig. 1A–D. For records see subspecies.

**Description (after Jamieson and Dyne 1976, and new subspecies below)**

Length 33–51 mm. Width (midclitellar) 1.7–2.2 mm. Segments 114–142. Form uniformly circular in cross-section throughout; pigmentless buff in alcohol. Prostomium epilobous 1/3. First dorsal pore 7/8 or 8/9. Setae 8 per segment, in regular longitudinal rows throughout, setae *a* and *b* of XVII and XIX modified as penial setae; setae *a* and *b* modified as spermathecal genital setae in VII, or VIII, or VIII and IX, but absent from XVIII. Nephropores inconspicuous on the clitellum in the vicinity of *d* lines. Clitellum annular, strongly developed, XII, XIII–XVII; setae visible on the clitellum, intersegmental furrows faint, dorsal pores obscured. Male pores minute orifices in seminal grooves, in mid-XVIII or just anterior to the setal arc; prostatic porophores 2 pairs, in XVII and XIX, on slight protuberances forming the four corners of a roughly square or laterally concave male field; within the male field a diamond arrangement of small elliptical markings, each a slightly glandular area with pore-like centre, in 17/18 and 18/19; or 3 of tubercles: a larger pair in XVIII (between the male pores), and 2 smaller pairs at 17/18 and 18/19 that are more closely adpressed. Other genital markings: a large transversely elliptical tumescence mid-ventrally in XVI with or without a pair of tubercles; paired markings also present in the vicinity of 19/20; other markings may be present including 15/16. A large pair of glandular swellings in each segment containing genital seta follicles. Female pores in *ab* (closer to *a* or in mid-*ab*) in XIV near intersegment 13/14. Spermathecal pores 2 conspicuous pairs, closely paired in *a* lines or *ab* in 7/8 and 8/9.

Some anterior septa thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII, supraoesophageal vessel IX–XIII; commissurals in X–XIII latero-oesophageal. Gizzard small to medium, or large, though compressible, in V; oesophagus lacking calciferous glands; intestinal origin in XV, a definite typhlosole absent or a low dorsal ridge commencing in XXII. Nephridia stomate holonephridia throughout; no anterior tufting demonstrable. Holandric; testes and funnels in X and XI; seminal vesicles 2 pairs, in IX and XII. Coiled, tubular prostate glands 2 pairs, in XVII and XIX, with stout or weakly muscular ducts, the anterior pair

of glands conspicuously the larger. The ventral body wall in the region of the male field (always?) with a raised glandular mass which receives the ectal ends of the vasa deferentia and prostatic ducts. Penial setae moderately long, ectally tapering shafts with some irregular blunt toothings on the distal eighth or lacking regular ornamentation. Length of mature seta = 1.54–1.58 mm; midshaft diameter = 18.0–19.2  $\mu$ m. Ovaries, and funnels, in XIII. Spermathecae 2 pairs, subequal, in VIII and IX, each comprising an ovoid ampulla joined by a short stalk to a clavate or lobed diverticulum the walls of which are typically packed with innumerable iridescent spheroidal sperm chambers. Length right spermatheca of IX 0.9–1.5 mm. Genital seta follicles moderate-sized to conspicuous; the setae stout shafts conspicuously ornamented with deep longitudinal notches which become more elongate entally; length of mature seta 0.53–0.65 mm, midshaft diameter 20.5–22.2  $\mu$ m.

*Diploptrema tyagarah tyagarah* Dyne, 1979b  
(Figs 94, 95)

*Diploptrema tyagarah tyagarah* Dyne, 1979b: 38–41, fig. 1A–D.

**TYPE LOCALITY:** (1) Qld, 30°07'S 149°49'E, 26 km north of Narrabri on Newell Highway, New South Wales, in black moist clayey soil under dry grass, W. Nash and R. Raven, 19 Jul 1975.

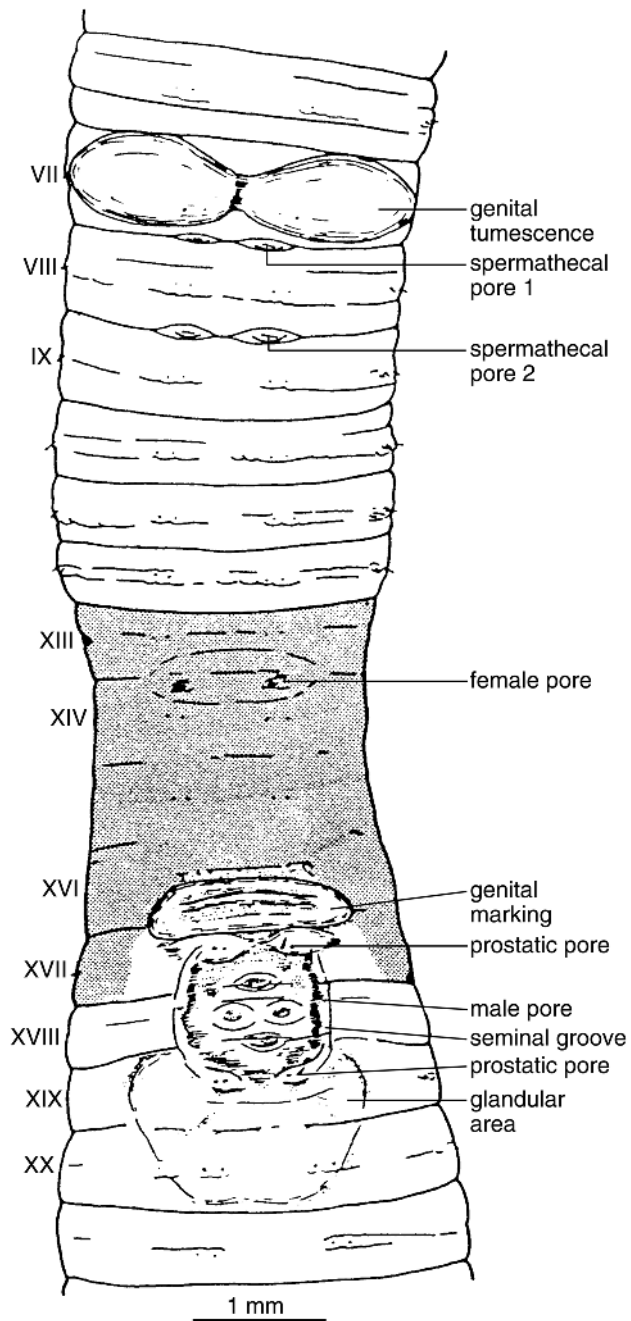
**PARATYPE LOCALITIES:** (1) As above. (2) Qld, 29° 49'S 149° 37'E, 42 km south of Moree on Newell Highway, in black clayey soil, just below surface in flat grassy country. Coll. W. Nash and R. Raven, 19 Jul 1975.

**HOLOTYPE:** (1) AM W 6622.

**PARATYPES:** (1) AM W 6623; (2) 6624.

**Description (after Dyne 1979b)**

Length >49.5 (posterior amputee) –51 mm. Width (midclitellar) 2.1–2.2 mm. Segments >71–142. Form uniformly circular in cross-section throughout; pigmentless buff in alcohol. Prostomium epilobous 1/3, peristomium somewhat furrowed. First dorsal pore 7/8. Setae 8 per segment, in regular longitudinal rows throughout, setae *a* and *b* of XVII and XIX modified as penial setae; setae *a* and *b* modified as spermathecal genital setae in VII but absent from XVIII. Nephropores inconspicuous on the clitellum (in *cd*?). Clitellum annular, strongly developed, XII (extending dorsally into ½XII)–XVII; setae visible on the clitellum, intersegmental furrows faint, dorsal pores obscured. Male pores minute orifices in broad seminal grooves, in mid-XVIII, slightly lateral of *b* lines; prostatic porophores 2 pairs, in XVII and XIX, on slight protuberances forming



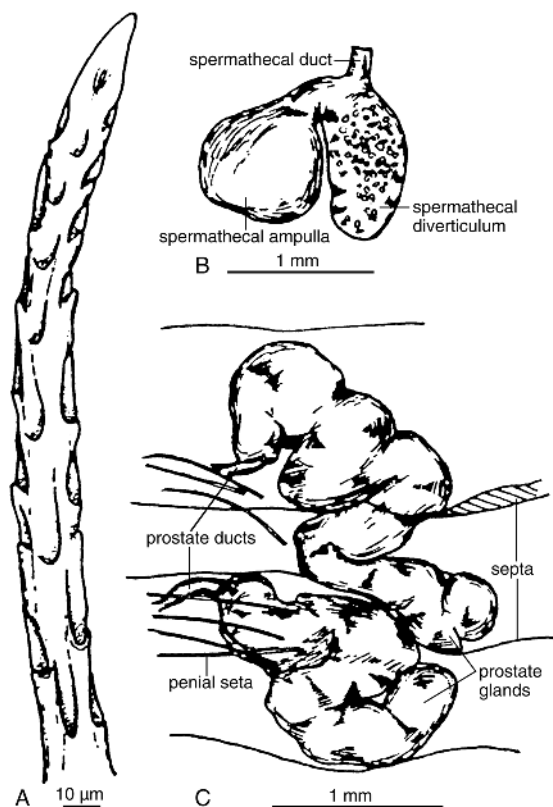
**Fig. 94,** *Diploptrema tyagarah tyagarah* Dyne, 1979, Holotype, genital field.

[After Dyne1979b]

the four corners of a roughly square male field, delimited laterally by a pair of broad seminal grooves joining the prostatic porophores; within the male field a diamond arrangement of small elliptical markings, each a slightly glandular area with pore-like centre, in 17/18 and 18/19; a large transversely elliptical tumescence with raised rim and median ridge, with slightly sunken centre in XVI, pressing anteriorly to meet the indented posterior edge of the clitellum; a diffusely glandular area immediately posterior to the male field, extending to 20/21, and within it, a faintly visible marking, similar to those within the male field, median, in XIX, close to 19/20. A large pair of glandular swellings in VII associated with the genital seta follicles, extending laterally to *c*, and filling the segment. Female pores conspicuous presetally in *ab* (closer to *a*) near intersegment 13/14, in XIV, surrounded by an

elliptical, paler region on the clitellum. Spermathecal pores 2 pairs, closely paired in *a* lines in 7/8 and 8/9, on protuberant lips.

Septa 6/9–10/11, slightly thickened, 6/7–8/9 moderately strongly thickened 5/6 moderately thickened. Dorsal blood vessel single, continuous onto pharynx. Last hearts in XIII, supra-oesophageal vessel IX–XIII, adherent to roof of oesophagus; commissurals in X–XIII larger than the remainder, and sending a narrow connective to both the dorsal and supra-oesophageal vessels, remaining commissurals very small and dorsoventral only. Gizzard small to medium, soft and compressible, in V; oesophagus VI–XIV, rather narrow, not well vascularised, with conspicuous rugae on its inner walls; intestinal origin in XV, with abrupt expansion, a definite typhlosole absent. Nephridia stomate holonephridia throughout, the medium sized nephrostomes preseptal and usually in *ab*; the wide, thin-walled ducts entering the parietes slightly pre-setally in *cd*; the nephridial body invested in a high peritoneum appearing as a very discrete sheaf of tissue in each segment; no tufting demonstrable in the pharyngeal region. Holandric; large flocculent sperm masses and very large, brightly iridescent sperm funnels in X and XI; seminal vesicles rather indefinite, but 2 pairs, one very small pair in IX, and a more prominent mass in XII, with apparent stem-like connection to the funnels of the preceding segment. Coiled, tubular prostate glands 2 pairs, in XVII and XIX, somewhat flattened, and with stout muscular ducts, the anterior pair conspicuously the larger, encroaching into XVIII. Penial seta follicles thin and transparent, with little copulatory musculature; *a* and *b* follicles conjoined; the setae moderately long, ectally tapering shafts with some irregular blunt toothing on the distal eighth. Length of mature seta = 1.54 mm; midshaft diameter = 19.2  $\mu$ m (H, mean of 3). Ovaries, comprising small sheaves of oocytes, and large, pleated funnels, in XIII. Spermathecae 2 pairs, subequal, in VIII and IX, each comprising a bulbous, ovoid ampulla joined by a short stalk to a clavate diverticulum, the walls of which are packed with innumerable iridescent spheroidal sperm chambers; whereas the ectal duct and diverticulum appear continuous, the stalked ampulla appears to be an appendage. Length right spermatheca of IX (apex ampulla to pore) = 1.5 mm ratio total length : length of duct = 5.6; ratio length: length diverticulum = 1.4. Genital seta follicles conspicuous in VII, *a* and *b* follicles inseparable; the setae stout shafts conspicuously ornamented with deep longitudinal notching which



**Fig. 95.** *Diploptrema tyagarah tyagarah* Dyne, 1979. Holotype: **A**, genital seta; **B**, right spermatheca of IX; **C**, right prostate. [After Dyne 1979b]

becomes more elongate entally; length of mature seta 0.65 mm, midshaft diameter 22.2  $\mu$ m (H, mean of 2).

### Remarks

*D. tyagarah tyagarah* is the only representative of *Diploptrema* known from New South Wales, and thus marks the point of the most southerly incursion of the genus in the eastern states. It is readily accommodated in the tightly knit *D. fragilis* species-group (refer to description of *D. quasifragilis* for definition of the latter), and, like the other members of the group, is an inland form.

The occurrence of the subspecies *D. tyagarah carnarvoni* in the Carnarvon Ranges, some 400 km to the north is of especial interest, in that this clearly demonstrates a past continuity that, due to increasing aridity, now no longer exists. It may be distinguished from other members of the species-group in having a well-developed gizzard, comparatively short prostate glands, no genital seta glands, and seminal vesicles in IX and XII.

### *Diploptrema tyagarah carnarvoni* subsp. nov.

**TYPE LOCALITY:** Central mid-W Qld, 25°03'S 148°14'E, near Camp Carnarvon water pump, on the bank of Carnarvon Creek, under weeds. Coll. E. Bradbury, 18 Dec 1971.

**HOLOTYPE:** QMGH 2905

**PARATYPES:** QMGH 2906–2908.

### Description

Length 33, 35 mm. Width (midclitellar) 1.7, 2.0 mm. Segments 114, 121, (H, P1). Body uniformly circular in cross-section throughout, pigmentless buff in alcohol, clitellum orange-pink. Prostomium epilobous 1/3, tongue rounded. First dorsal pore 8/9 (H, P1). Setae 8 per segment, ventral setal couples of XVIII absent, those of XVII and XIX modified as enlarged penial setae; those of VIII (H) or VIII and IX (P1) modified as genital setae. Nephropores barely visible as small points in the clitellar region, equatorial, roughly in alignment with *d* lines. Clitellum annular, over XIII–XVII, interrupted ventrally in XVI and XVII by the male field, and a large tumescence median in XVI; dorsal pores and intersegmental furrows obscured, setae visible. Male pores minute orifices at the ventral margins of the seminal grooves, just anterior to the setal arc, in XVIII. Prostatic pores on low mounds, the pores of a side conjoined by a seminal groove, which is very slightly convex laterally. The male field, as delimited by the seminal grooves, and the lines joining the prostatic pores of a segment, is slightly concave, and

contains a number of raised tubercles, 3 pairs in all: a larger pair in XVIII (between the male pores), and 2 smaller pairs at 17/18 and 18/19 that are more closely adpressed. Genital markings a single, large, median pad consisting of a pair of tubercles immediately anterior to the porophores (in XVI), conjoined by a raised glandular strip (present in all specimens); a more closely paired set of markings is present immediately posterior to the prostatic pores of XIX, in 19/20 (present in all specimens, occasionally (P5–6) fused to form an unpaired median marking; the three pairs of tubercular markings within the male field are always present, with the rare variation (P2) of a duplication of the XVIII markings to produce a compact cluster of 4 tubercles; exceptionally (P5), the paired markings of 17/18 and 18/19 are fused, to produce single median swellings; a small, median tumescence in 15/16 is occasionally present (P2 — faint, P3, P5); the swellings characteristically associated with genital setae are invariably present in VIII, exceptionally (P1) in IX additionally. Female pores small openings, near 13/14, in XIV, in line with mid *ab*. Spermathecal pores 2 conspicuous pairs (not closely associated), in *ab*, in 7/8 and 8/9.

Septa 5/6 delicate, 6/7 slightly thickened, 7/8–9/10 moderately muscularised, 10/11–11/12 slightly thus. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X–XIII true latero-oesophageal hearts, though the commissurals of X and XI are rather slight; remainder dorso-ventral only, and very thin; supra-oesophageal vessel detected in X–XIII only. Gizzard large, muscular, and barrel-shaped, though compressible, in V, deflecting posteriad septa 5/6 and 6/7 only; oesophagus narrow, moniliform, in VI–XIV, calciferous glands and pouching absent. Intestine commences with abrupt expansion in XV, the typhlosole represented by a low, dorsal ridge, which appears in XXII. Holonephric throughout, each nephridium stomate and avesculate, with long, delicate nephrostomal necks, and thin-walled ducts entering the parietes presetally in *d* lines; nephridial bodies apparently invested in a high peritoneum giving the appearance of discrete, foliose units. Anterior tufting not demonstrable. Holandric; 2 pairs of medium-sized funnels and adherent sperm masses present in X and XI; 2 pairs of large seminal vesicle masses located in IX and XII, each divided up into large, rounded loculi; vas deferens clearly visible on the body wall (particularly in the clitellar region) as rather straight, closely paired, iridescent tubes. The ventral body wall in the region XVII–XX with raised glandular tissue; the vasa deferentia and prostatic ducts disappear into this glandular mass.

Prostate glands tubular, the anterior pair (origin XVII) extending into XX, and clearly larger than the posterior set, which extends to XXI; neither set of glands is highly convoluted, but loosely coiled; the ducts are straight and weakly muscular. Penis setal follicles of moderate size, each containing at least 3 reserve setae in various stages of growth; the follicles are ligamented to the dorsal aspect of the body wall; the setae with moderately strong bending, simple, entire, lacking regular ornamentation of any kind, attenuating gradually. Length of mature seta 1.58 mm; midshaft diameter 18.0  $\mu$ m (mean of 3). Ovaries, consisting of bundles of large oocytes, and small oviducal funnels, present in XIII; spermathecae 2 subequal pairs, in VIII and IX, opening anteriorly in their respective segments; each organ consists of a sacciform ampulla, tapering proximally to join, after a tight bend, the lobe-like diverticulum; the latter is of approximately the same length as the ampulla, and is brightly iridescent; the short duct arises from the junction of the two components. Length right spermatheca of IX 0.9 mm (apex of ampulla to pore). Genital seta follicles of moderate size present in VIII (exceptionally, P1, present in IX as well), accessory glands absent; the setae gently curving, tapering gradually to a fine point, ornamented over the ectal  $2/5$  with the narrow scalloping typical of the species-group; length of mature seta 0.53 mm; midshaft diameter 20.5  $\mu$ m.

#### Remarks

Though close in many respects to the typical population, erection of the new subspecies is justified on the basis of the following consistent differences: *D. tyagarah tyagarah*/*D. tyagarah carnarvoni* (a) average body length 49 mm/34 mm; (b) genital setae in VII/in VIII (rarely in

both VIII and IX); (c) male field markings in the form of 3 pairs tubercles/a diamond arrangement of 4 units; (d) marking in 19/20 lacking/marking in 19/20 present; (e) gizzard small-medium/somewhat larger; (f) prostate glands of XVII extending to XIX/extending to XX.

As Dyne (1984, unpublished) notes, the Carnarvon Gorge area has generally been regarded as a moist refugium for animal and plant species that can no longer survive in the surrounding arid regions. These may have originally occupied much of the brigalow belt, but have contracted to more climatically stable habitats owing to interpluvial influence. That the hiatus between the two subspecies of *D. tyagarah* is real, rather than an artefact of differential collecting effort remains to be demonstrated conclusively. What is apparent, however, is that members of the *D. fragilis* group, if once widespread, have not taken advantage of the numerous closed forest habitats in SE Queensland/N New South Wales to which other genera (e.g. *Digaster*, *Spenceriella sensu lato*, *Heteroporodrilus*) have contracted during the current interpluvial. It is likely that a specific environmental requirement is implicated, but in view of the variables which might be involved (e.g. soil type, organic status, moisture content, altitude, temperature, etc.), a diagnosis in the short-term seems doubtful.

This subspecies is very close morphologically to *D. capella*. If *D. capella* were considered to be its senior synonym, the latter would have to be subsumed in *D. tyagarah* as a subspecies. This would not transgress the above argument concerning range, as *D. capella* was recorded from an artificially maintained site at Capella, near Emerald, questionably its natural habitat.

WESTERN AUSTRALIAN *DIPLOPTREMA* SPECIES***Diploptrema cornigravei* Michaelsen, 1907**

(Figs 96, 97)

*Eodrillus cornigravei* Michaelsen, 1907: 144.*Eodrillus cornigravei*; Jackson 1931: 82–83.*Diploptrema cornigravei*; Jamieson 1971b: 102.

**TYPE LOCALITY:** WA, 31°59'19"S 115°55'50"E, Cannington, in swampy ground. coll. W. Michaelsen.

**SYNTYPES:** USNM 021046 (fragments) (seen, BGMJ); WAMP 4403; MNHU 4219 (*vide* Reynolds and Cook 1976).

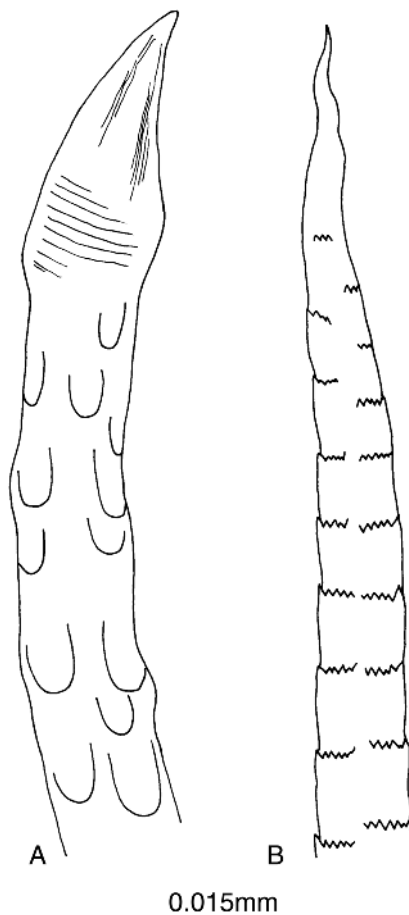
**Description (after Michaelsen 1907; Jackson 1931)**

Length 85 mm. Width 2 mm. Segments about 200. Grey and unpigmented, the white nephridia being visible through the skin. Setae closely paired;  $aa = cd = \frac{1}{4}aaa$ ;  $aa = bc$ ;  $dd = 0.6u$ . Epilobous. Dorsal pores not known. Nephridial pores of the anterior segments are immediately below the *c* line of setae, while further back they are in the line *cd*. Male pores not known and setae of XVIII all normal. Prostates open to the exterior in *ab* lines. Spermathecal pores 2 pairs in 7/8 and 8/9 immediately lateral to *a* lines; ventral setae of VIII and IX modified as genital setae, and marked on the distal half by 4 irregular longitudinal rows of low rounded scars. The distal tip is claw-like, swelling out slightly just before the point and marked by 2 longitudinal ridges.

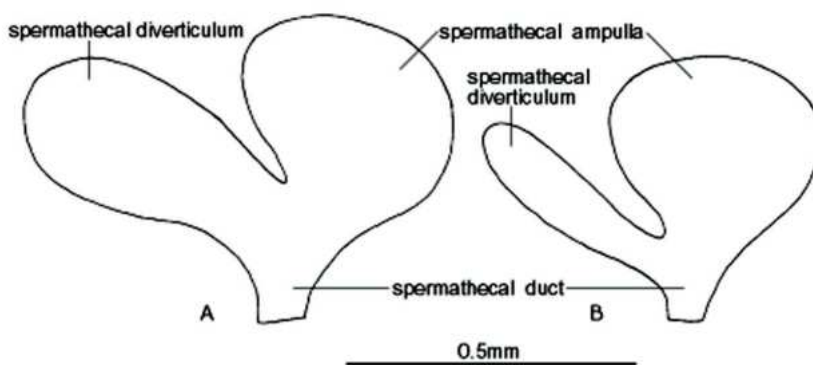
Septa 5/6–13/14 thickened. Gizzard in V; mid-gut begins in XIII. Last hearts in XII. Seminal vesicles, in IX and XII. Prostates long and thread-like, irregularly twisted at the proximal end. Penial setae in XVII and XIX; marked by scar-like grooves with irregularly toothed distal margins; the distal end irregularly bent and tapering to a sharp point. Spermathecae ampulla-shaped or sac-like, merging into the duct; a diverticulum with a sacculated lumen opens into the distal region of the ampulla.

**Remarks**

The above account is chiefly taken from the synopsis of Jackson (1931). This species, like the other known Western Australian species, *D. macleayi*, is in need of redescription.



**Fig. 96.** *Diploptrema cornigravei* Michaelsen, 1907: **A**, distal end of genital seta; **B**, distal end of penial seta. [Redrawn after Michaelsen 1907b]



**Fig. 97.** *Diploptrema cornigravei* Michaelsen, 1907: A, posterior spermatheca; B, anterior spermatheca. [Redrawn after Michaelsen 1907b]

### ***Diploptrema macleayi* (Fletcher, 1890)**

*Acanthodrilus macleayi* Fletcher, 1890: 999–1000.

**TYPE LOCALITY:** WA, Napier Range, 100 miles S of King's Sound, Coll. Mr W. Froggatt; about 110 specimens).

**SYNTYPES:** Macleay Museum (lost).

**FURTHER RECORDS:** NW Australia, Napier Range., many specimens. AM W 197357–197358. Ident. E. Easton 1983. (We have not had the opportunity to examine these. It is possible, as no collector is given, that they are the missing types.)

#### **Description (after Fletcher 1890)**

One of the largest specimens 27 mm long, 2 mm wide; segments about 90. Colour rather light yellowish-brown. Prostomium epilobous,  $<1/2$ . Setae: four pairs per segment after the first one, closely paired; the inner pairs on XVII and on XIX either not visible (probably then only obscured by the swellings on these segments) or situated a little dorsad of the usual position. Clitellum XII–XVI or XVII. 'Male' (i.e. prostate) pores two pairs, on XVII and XIX, the pores of each pair closer to the median line than *a* lines of adjacent segments. The ventral surface of XVI and XVII, and to a less

degree of the next two or three segments more or less modified and swollen as far dorsad as *bc*, the modified surfaces more or less confluent, but intersegmentally for a short distance on either side of the median line less modified; the three or four intersegmental depressions (the first one between XVI and XVII) so commonly present in spirit specimens are probably *post-mortem* and due to shrinkage. Female pores, spermathecal pores, nephropores, and dorsal pores not determinable.

A single large gizzard. Holonephric. A large pair of seminal vesicles (probably in XII), a doubtful smaller pair in IX, with two pairs of seminal funnels (and probably testes) in X and XI. Prostates 2 pairs, with straight fairly long ducts, Four pairs of delicate sacs, a pair to each prostate duct, containing penial setae, long, curved, and tapering, and minutely notched distally, the free extremity not a sharp point, but flattened.

#### **Remarks**

This was the only species of earthworm obtained by the collector, W. Froggatt, during nearly a year's residence in the Kimberley District (Fletcher 1890). The above account paraphrases that of Fletcher.

NORTHERN TERRITORY *DIPLOPTREMA**Diploptrema armatissima* Jamieson  
and Dyne, 1976

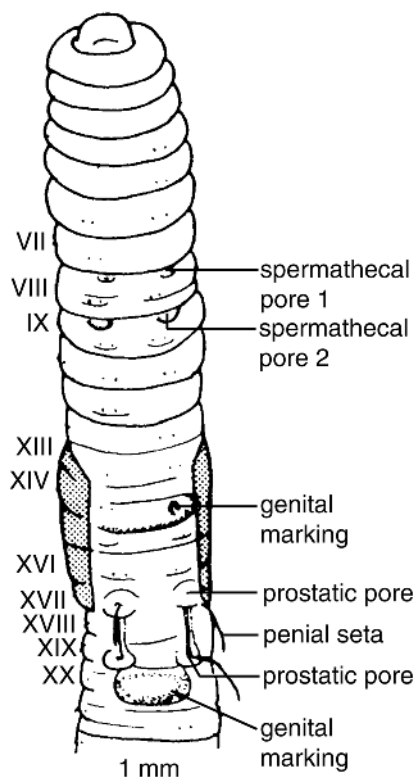
(Figs 98, 99, 101A,B)

*Diploptrema armatissima* Jamieson and Dyne, 1976:  
450–452, figs 1, 2b, 9a, 10a, 11, 12, table 1.**TYPE LOCALITY:** NT, 12°21'S 130°53'E,  
Casuarina Hospital site, Darwin, rain forest soil.  
Coll. W. Nash and M. Shand, 11 Dec. 1974.**HOLOTYPE:** QM G8382**PARATYPE:** QM G8383**Description (after Jamieson and Dyne 1976)**

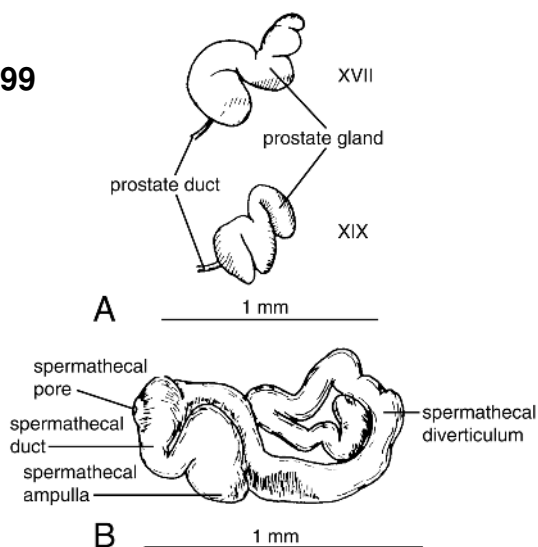
Length 21–28 mm. Width (midclitellar) 1.0–1.1 mm. Segments 77–104 (H, P1). Proepilobous. First dorsal pore 8/9 (imperforate?), 9/10 or 12/13 (perforate). Some tumescence present (sometimes absent) around setae *ab* in IX and postsetally in VIII, but no genital setae apparent in internal dissection. In XII, *aa: ab: bc: cd: dd:* 4.5: 1.0: 4.5: 0.8: 18.1; *dd: u* = 0.53. Nephropores not externally recognisable. Clitellum saddle-shaped, strongly protuberant, in XIII–XVII, ventral margins below *a* lines. Prostatic pores in *ab* nearer *b*, on small subcircular porophores; male pores faint points anteriorly in XVIII, approximately in *a* lines; seminal grooves indistinct, straight, in *b* lines; the anterior prostatic pores 0.5 mm, 0.17 body circumference apart. Genital markings an inter-segmental tumescence with pore like centre in *ab* in 14/15, on the left or right that of the holotype extending across the ventral midline; a similar marking on the left in 26/27. Female pores not discernible. Spermathecal pores in *a* lines, on small papillae, the posterior pair 0.48 mm, 0.15 body circumference apart.

Thickest septa 7/8–10/11, moderately thickened. Supra-oesophageal vessel visible in VII–XII. Last hearts in XIII, at least those in X and XI shown to be latero-oesophageal. Gizzard large, strongly muscular but compressible, widening to an anterior rim in V. Oesophagus lacking calciferous glands. Intestinal origin uncertain, apparently XV, transition from the oesophagus indefinite, not wide and thin-walled until XVII or XVIII; a low dorsal typhlosole commencing in XXV. Nephridia commencing in II; none tufted though those in IV and V are larger and more coiled than others; ducts entering the parietes presetally in *d* lines; preseptal funnels demonstrated in the anterior intestinal region. Iridescent free sperm funnels in X and XI; seminal vesicles racemose in XI and XII. Prostates 2 subequal pairs restricted to either XVII or XIX: depressed tubular, almost rudimentary; duct short and slender. Penial setae with conspicuous

98



99



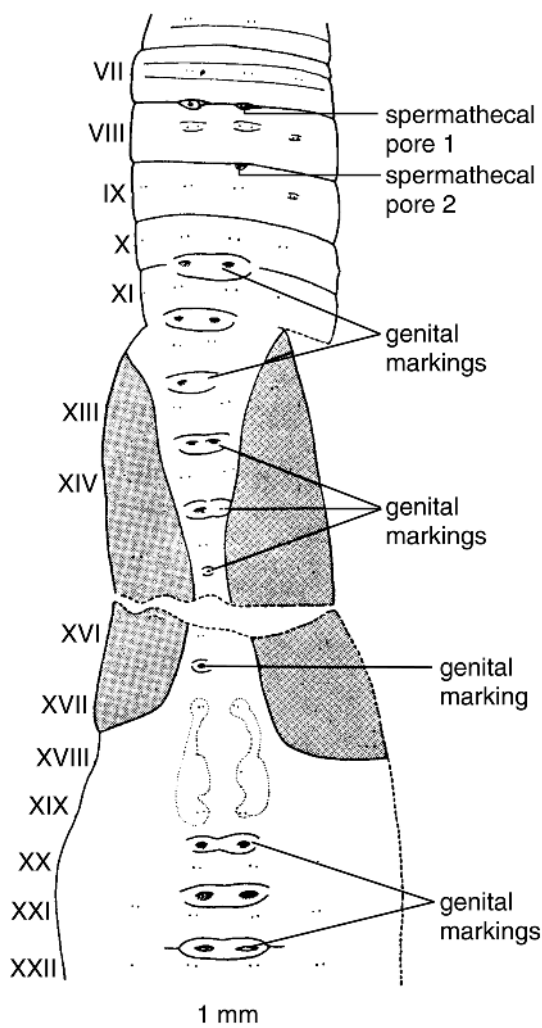
**Figs 98, 99, *Diploptrema armatissima* Jamieson and Dyne, 1976, Holotype: A, right prostates; B, right spermatheca of IX.** [After Jamieson & Dyne 1976]



separate *a* and *b* follicles; exceptionally long, extending posteriorly on the body wall to XXXIX or XXXVII; setae with extremely long, thin shafts, the apical region irregularly covered with groups of distally directed triangular teeth; length of a mature seta 12.12 mm; midshaft diameter 13.6  $\mu$ m. Ovaries with few large terminal oocytes; large multiloculate ovisacs in XIV. Spermathecae 2 subequal pairs, ampulla distorted ovoid with short duct which is joined ectally by a long, coiled tubular diverticulum in such a way that the ampulla appears an appendage of the diverticulum; the diverticulum widening greatly ectalwards, approximately its ental half iridescent owing to free(?) sperm masses, no seminal chambers evident; the wide base of the diverticulum, after receiving the ampulla, sessile on the body wall; length right spermatheca of IX 0.7 mm; ratio total length: length duct = 1.7; ratio total length: length diverticulum = 0.3.

#### Remarks

*D. armatissima* belongs to a group of species (including *D. insularis*, *D. melaleucae* and *D. intermedia*) with long and often coiled tubular spermathecal diverticula. It differs from *D. insularis* and *D. melaleucae* in lacking their characteristic intersegmental accessory genital markings. Nevertheless, *D. intermedia* is morphologically very close; synonymy with *D. armatissima* requires consideration when further material becomes available from the type, and intermediate, localities. At present *D. armatissima* is considered specifically distinct from *D. intermedia* in the disposition of genital markings and the presence of seminal vesicles in both XI and XII.



**Fig. 100.** *Diploptrema eremia* (Spencer, 1896), genital field of Syntype HM V6909.

[After Jamieson and Dyne 1976]

### *Diploptrema eremia* (Spencer, 1896)

(Fig. 100)

*Acanthodrilus eremius* Spencer, 1896: 418–420, pl. 29, figs 1–5.

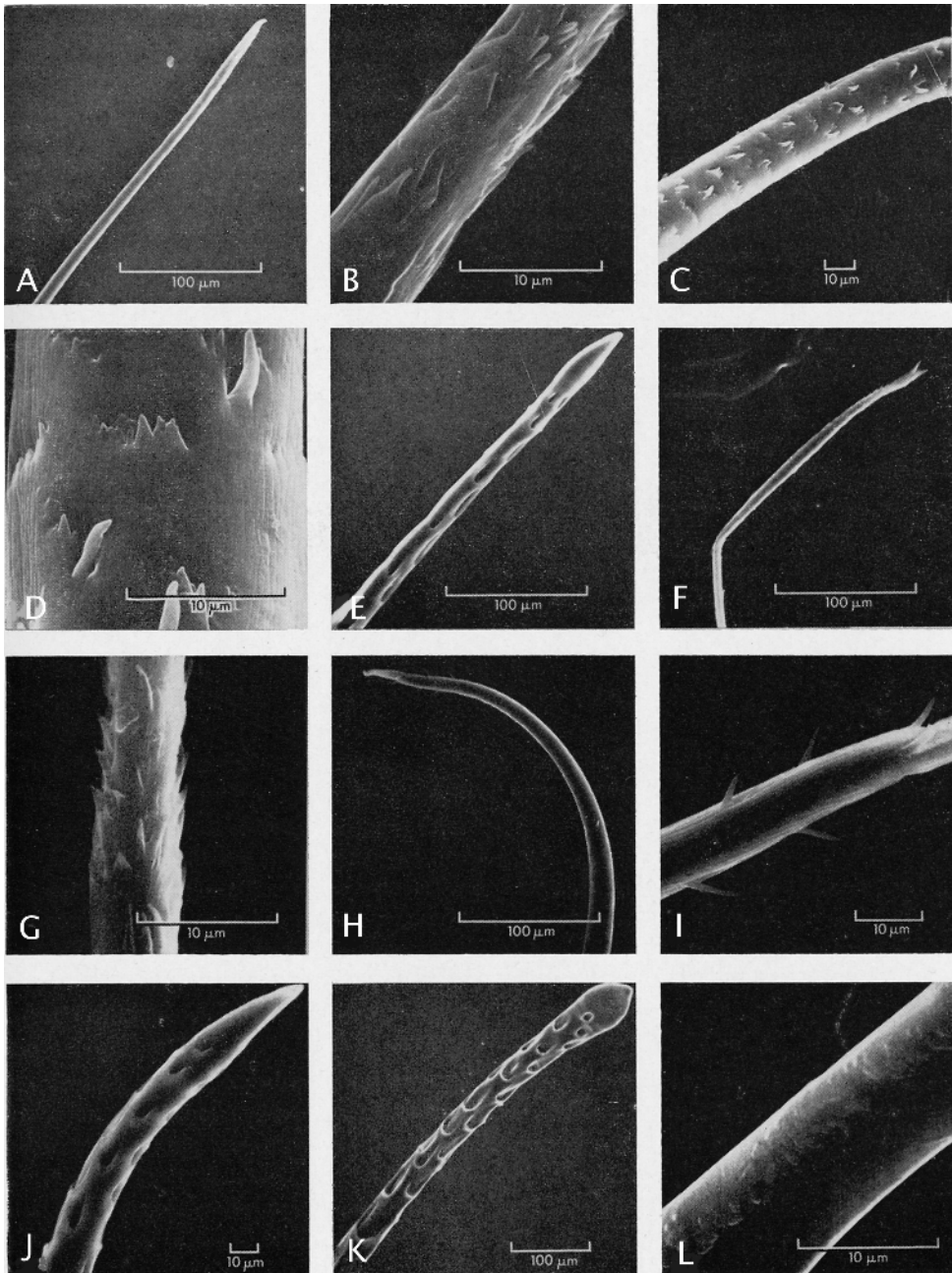
*Notiodrilus eremus*; Michaelsen 1900: 137.

*Notiodrilus eremius*; Jamieson 1971b: 102.

*Diploptrema eremia*; Jamieson and Dyne 1976: 452–454, figs 1, 4a, table 1.

**TYPE LOCALITIES:** NT, 24°18'S 132°41'E, Illamurta, James Range; NT, 24°24'S 131°47'E, Bagot's Creek, George Gill Range; NT, 23°40'S 132°43'E, Finke Gorge, McDonnell Range.

**SYNTYPES:** HMV 6909 (re-examined). USNM 021048.



**Description (after Spencer 1896; Jamieson 1971b; Jamieson and Dyne 1976)**

Length 77–85 mm. Width 2 mm. Segments 180. Epilobous 1/2. First dorsal pore postclitellar. Genital setae present in VIII and IX; in XI, *aa: ab: bc: cd: dd* = 4.8: 1.0: 4.6: 0.7: 30; *dd: u* = 0.63. Nephropores, from internal examination, in *d* lines [location in *ab* reported by Spencer appears erroneous]. Clitellum well developed, XII, XIII–½XVIII, XVIII, saddle-shaped, interrupted ventrally throughout its length or incomplete ventrally only in XVII and XVIII. Male and prostatic pores slightly ventral of *a* but setae *a* and *b* absent in XVIII; seminal grooves(?). Genital markings: paired elliptical tumid patches may be present in some or all of intersegments 17/18, 18/19, 19/20, 20/21 and 21/22; those in 19/20–21/22 may be transversely conjoined and have pore-like centres slightly median to *a* lines; in addition similar paired, or, exceptionally, unilateral, markings may occur in intersegments 10/11–16/17. Female pores shortly anterolateral of setae *b*. Spermathecal pores in *ab*, on small papillae.

Last hearts in XIII, latero-oesophageal, with a well-developed supra-oesophageal vessel. Dorso-ventral commissurals commencing in V. Gizzard in V; large but readily compressible and musculature tending to become vestigial. Intestinal origin XVII; typhlosole not demonstrable. Holonephridia commencing at the anterior extremity, the slender avesculate ducts discharging presetally in *d* lines. 'Peptonephridia' were reported by Spencer. Holandric: iridescent sperm funnels in X and XI. Prostates tubular, both pairs extending to XX or XXII; the anterior pair the larger. Penial setae long and thin with separate *a* and *b* follicles which extend into XXIV; ornamentation absent. Genital setae sculptured, including the deep regular notching on all sides. Seminal vesicles racemose, in IX and XII. Ovaries fan-like with many strings of large oocytes; ovisacs present on the anterior septum of XIV above the oviducal funnels. Spermathecae with ampulla and two diverticula, one a small knob-like process close to the pore, the other a long tubular and at times somewhat coiled process which may be as long as or longer than the ampulla. In some type material the spermathecal duct is unusually long, slender, and tortuous; the single diverticulum is simple and not appreciably

different in size from the ampulla, differing from the latter in having a lobulate outline owing to internal sperm chambers.

**Remarks**

Until material of *D. cornigravei* and *D. queenslandica*, which also have seminal vesicles in IX and XII, is rediscovered, it will not be possible to establish whether they are synonymous with the earlier described *D. macleayi*.

The species closest to *D. eremia* is *D. shandi*, also with seminal vesicles in IX and XII, but the latter differs notably in location of the first dorsal pore in 7/8, in its setal ratios, the characteristic form of the ventral accessory genital marking at 16/17, and the frequency distribution of the accessory markings.

***Diplotrema insularis* Jamieson and Dyne, 1976**

(Figs 101C–E, 102, 103)

***Diplotrema insularis*** Jamieson and Dyne, 1976: 454–456, figs 1, 3a, 9b, 10b, 13, 14, 15, table 1.

**TYPE LOCALITY:** NT, 11°21'S 130°26'E, 3 km N of Garden Point, Melville Island.

**PARATYPE LOCALITY:** NT, 11°22'S 130°26'E, 1.5 km N of Garden Point

**HOLOTYPE:** (1) QM G8384

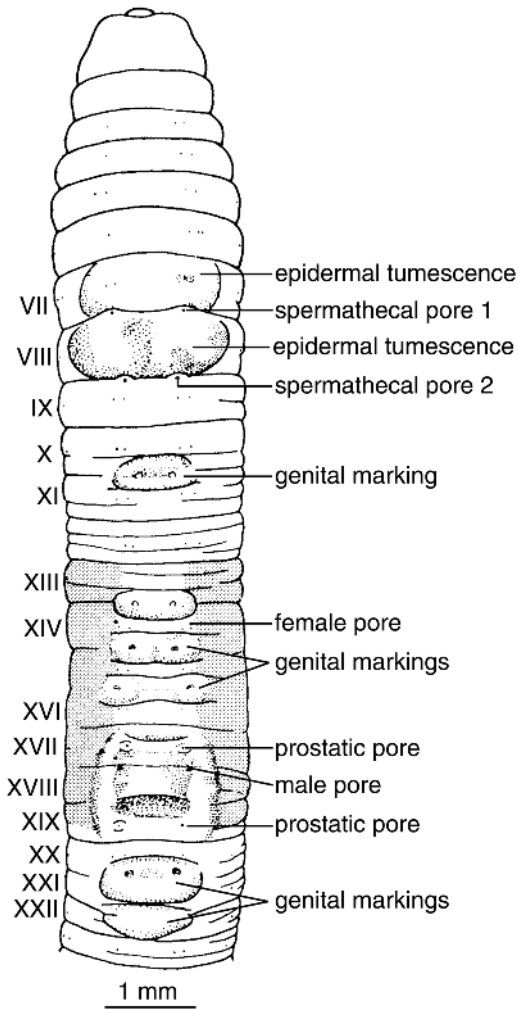
**PARATYPES:** (1) QM G8385–8387, AM W6603, 6604; (2) QM G8388–8392.

**Description (after Jamieson and Dyne 1976)**

Length 65–71 mm. Width (midclitellar) 2.0 mm. Segments 189–218. Epilobous 2/3 open, strongly convergent posteriad. First dorsal pore 9/10. Genital setae present in VIII, or, less commonly, VII and VIII; in XII, *aa: ab: bc: cd: dd* = 5.6: 1.0: 6.8: 0.8: 36.2; *dd: u* = 0.62. Nephropores not externally visible. Clitellum saddle-shaped, XIII–⅔XIX, XIX. Prostatic pores 2 pairs, in *a* lines on minute papillae; seminal grooves indistinct, almost inappreciably convex laterally to very slightly lateral of *b* lines; male pores minute at the anterior margin of XVIII in *b* lines. Prostatic pores of XVII 0.63 mm, 0.10 body circumference apart. Genital markings are present intersegmentally in the following order of decreasing frequency: in intersegment 13/14, 14/15, and 15/16 (constant); in 21/22 (very frequent); in 10/11 (frequent); in 11/12 and 19/20 (less than half the specimens); in 21/22, 16/17 and/or 18/19 (exceptionally); and in 12/13 or 17/18 (very rarely). The markings in 10/11 to 17/18 are a pair of circular prominences in each intersegment, with pore-like centres in or slightly

**Fig. 101.** Penial and genital setae in *Diplotrema*: **A, B**, *D. armatissima*, penial seta; **C, D**, *D. insularis*, penial; **E**, *D. insularis*, genital; **F, G**, *D. intermedia*, penial; **H, I**, *D. mantoni*, penial; **J**, *D. mantoni*, genital; **K**, *D. melaleuca*, genital; **L**, *D. minuta*, penial.

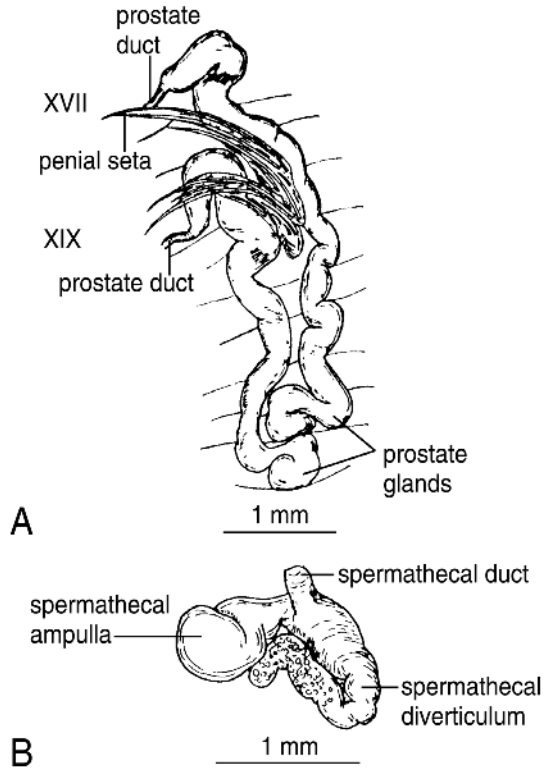
[After Jamieson and Dyne 1976]



**Fig. 102.** *Diploptrema insularis* Jamieson and Dyne, 1976, Holotype, genital field.

[After Jamieson and Dyne 1976]

median of *ab*, usually conjoined midventrally and in some individuals present only unilaterally; the marking in 18/19 is paired, or paired with an additional midventral marking, and the marking in each of 19/20, 20/21 and 21/22 consists of a midventral unpaired transverse pad with a pair or a triplet of, or no pore-like areas. A pair of tumescences (usually conjoined midventrally) associated with the spermathecal genital setae is constant in VIII and is exceptionally present in VII. Female pores in or slightly lateral of *b* lines (asymmetrical) shortly presetally in XIV. Spermathecal pores on small papillae, in *a* lines; the posterior pair 0.60 mm, 0.09 body circumference apart.



**Fig. 103.** *Diploptrema insularis* Jamieson and Dyne, 1976, Holotype: **A**, prostates; **B**, left spermatheca of IX. [After Jamieson and Dyne 1976]

Thickest septa 6/7–9/10, moderately thickened. Supra-oesophageal present in VIII– $\frac{1}{2}$ XIV; last hearts in XIII latero-oesophageal in X–XIII; dorsoventral commissurals in VI–IX. Gizzard fusiform, large, but readily compressible, in V. Oesophagus wide and moderately vascular in VIII–XI; much widened and conspicuously vascularised in XII–XV, in which it is internally rugose, but calciferous glands absent; pale and narrow in XVI. Intestinal origin XVII, a low laminar dorsal typhlosole commencing in XXV. Nephridia commencing in II; those in IV and V forming very large tufts with many spiral loops; a duct from those of V passes forward into segment I, receiving a duct from the tuft in IV and the small tufts in III and II, on each side, the common duct ending in the vicinity of the mouth but whether exonephric or enteronephric not determined. Nephridia in VI much coiled but, like the succeeding nephridia, which are progressively less coiled and soon become simple, discharging anteriorly in their segments far lateral of *d* lines; preseptal funnel very small, demonstrated in the

anterior intestinal region. Large strongly iridescent free sperm funnels in X, and XI; large racemose seminal vesicles in XI and XII, those in XII the larger. Prostates long, tubular and loosely coiled, extending posteriorly into XXVI; the anterior pair slightly the larger. Prostatic ducts slender not conspicuously muscular tubes, widening gradually towards the body wall; vasa deferentia iridescent, double on each side, winding on the internal parietes. Penial setae with separate *a* and *b* follicles forming conspicuous arcs, those of XIX extending into XXV. Setae gradually tapering shafts of moderate length, the ectal 1/10 ornamented with numerous regularly spaced, broad, jagged-edged bracts interspersed with larger teeth in groups of 1–3; length of mature seta 1.92 mm; midshaft diameter 15.2  $\mu$ m (P3, mean of 3). Genital setae small, with long, regularly arranged depressions closely spaced on the apical  $\frac{1}{3}$ ; length of mature seta 0.88 mm; midshaft diameter 19.7  $\mu$ m. Ovaries palmate with many egg strings; ovisacs absent. Spermathecae 2 subequal pairs, each with a long, thin-walled, ovoid, apically pointed ampulla, and a longer, coiled, tubular inseminated diverticulum with many flecks owing to numerous spherical sperm chambers in its walls. Length of left spermathecae of IX 1.5 mm; ratio of length : length duct = 2.1; ratio length : length diverticulum = 0.7.

#### Remarks

The constant location of paired, if conjoined, genital markings in intersegments 13/14, 14/15 and 15/16, and frequent presence of a marking in 10/11 and 21/22, combined with their much lesser frequency in other intersegments, distinguish *Diploptrema insularis* from other species of the genus.

### *Diploptrema intermedia* Jamieson and Dyne, 1976

(Figs 101F, G, 104, 105)

*Diploptrema intermedia* Jamieson and Dyne, 1976: 456–457, figs 1, 2c, 9c, 10c, 10d, 16, 17, table 1.

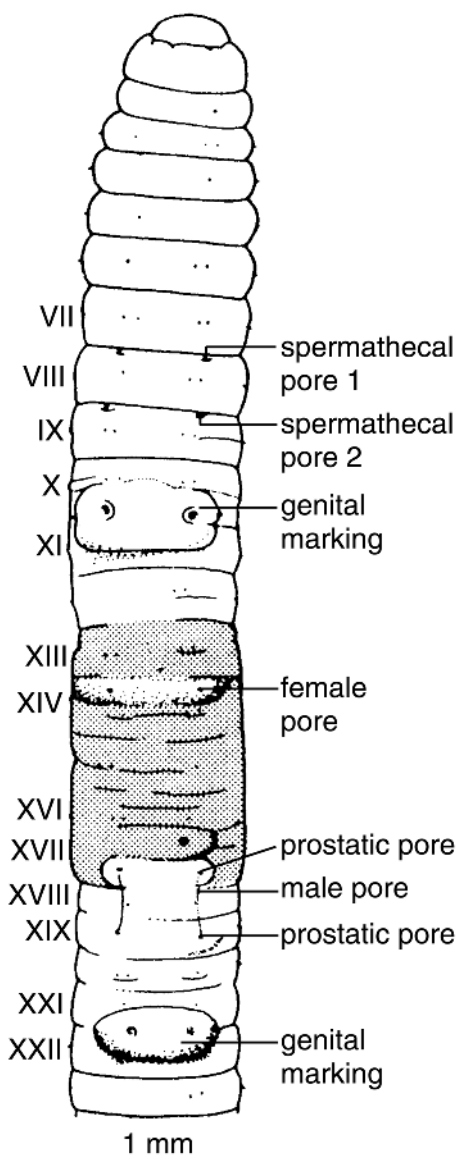
**TYPE LOCALITY:** (1) NT, 12°27'S 131°07'E, 7 km NE of Howard Springs.

**PARATYPE LOCALITIES:** (2) NT, 12°34'S 131°06'E, 5 km towards Humpty Doo from the Stuart Highway turnoff. (3) NT, 13°27'S 131°08'E, Robin Falls, 140 km S of Darwin.

**HOLOTYPE:** (1) QM G8393.

**PARATYPES:** (2) QM G8394; (3) QM G8395–8399.

#### Description (after Jamieson and Dyne 1976)



**Fig. 104.** *Diploptrema intermedia* Jamieson and Dyne, 1976, Holotype: **A**, right prostates; **B**, right spermatheca of IX; **C**, left spermatheca of IX.

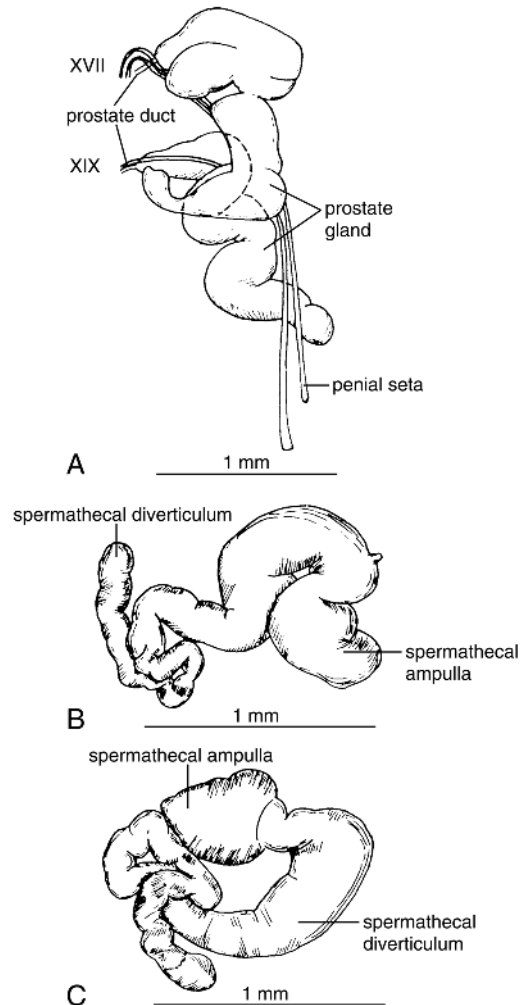
[After Jamieson and Dyne 1976]

Length 36–37 mm. Width (midclitellar) 1.1–1.3 mm. Segments 122–129. Epilobous 1/2 closed; strongly convergent posteriad. First dorsal pore 7/8. Genital setae or associated epidermal modification absent. In XII, *aa*: *ab*: *bc*: *cd*: *dd* = 8.7: 1.0: 7.6: 1.5: 33.5; *dd*: *u* = 0.54. Nephropores visible on the clitellum in *d* lines. Clitellum in XIII–XVII, weakly developed between setal lines *b*, very strongly protuberant

above these. Prostatic pores in *ab* nearer *b*; on indistinct porophores; male pores minute and indistinct at the anterior margin of XVIII, very slightly lateral of *b* lines; seminal grooves thin and faint, with narrow lateral tumid border, almost straight, curving almost imperceptibly towards the midline in XVIII and furthest median at its equator, immediately lateral of setae *b*; the prostatic pores of XVII 0.6 mm, 0.15 body circumference apart. Genital markings: a midventral subrectangular pad, with pore-like areas in *ab*, intersegmental but reaching at least the setal arcs of the adjacent segments, in one or more of 8/9, 10/11 and 12/13; paired (sometimes unilateral) circular intersegmental markings with pore-like centres in one or more of 13/14; 14/15; 16/17; 19/20 or typically conjoined to give a large pad 21/22. Female pores in *b* slightly nearer the anterior margin than the setal arc of XIV on a transverse tumescence with wing-like lateral extremities. Spermathecal pores immediately lateral of *b* lines with slight posterior protuberant lip; the posterior pair 0.68 mm, 0.17 body circumference apart.

Thickest septa 6/7 and 7/8, moderately strongly thickened. Supra-oesophageal vessel present in at least IX–XII, slender and indistinct and precise limits indeterminable. Last hearts in XIII. Gizzard large, in V, elongate-cylindrical with anterior rim, but fairly easily compressible. Oesophagus in XII–XVI segmentally dilated and richly vascularised; not notably so in VI–XI; narrow and pale in XVII; gut slightly dilated in XVIII and XIX; thick-walled and presumably oesophageal in XVIII, thin-walled and apparently intestinal in XIX, though not strongly dilated until XX; dorsal typhlosolar ridge very rudimentary, commencing in XXVIII. Nephridia in II–VII and especially VI and VII, enlarged and complexly coiled but not tufted; ducts entering the parietes in *d* lines; funnels demonstrated in VI and in the anterior intestinal region. Large iridescent free sperm funnels in X and XI; seminal vesicles racemose, in XII only. Prostates 2 subequal pairs, depressed tubular, restricted to a single segment or (a posterior prostate) winding posteriorly into XXII; ectal duct short and slender. Penial setae in conspicuous, exceptionally long follicles, those of XVII and XIX tightly bent at the prostate ducts and then running straight posteriorly on the body wall to enter segments XXVIII and XXX respectively; *a* and *b* follicles present but conjoined; the setae with extremely attenuate shafts, the distal region clothed irregularly with very sharp projecting teeth; length of mature seta 11.66 mm; midshaft diameter 15.2  $\mu$ m (mean of 2). Ovaries wisp-like with several conjoined egg strings; sacs on the anterior septum of XIV are

presumably ovisacs. Spermathecae subequal; ampulla distorted ovoid with short duct which is joined ectally by a longer coiled tubular diverticulum in such a way that the ampulla appears as an appendage of the diverticulum; the diverticulum widening greatly ectalwards; approximately its ental third being iridescent owing to sperm masses which appear to be free in the lumen; the wide base of the diverticulum, after



**Fig. 105.** *Diploptrema intermedia* Jamieson and Dyne, 1976, Holotype: **A**, right prostates; **B**, right spermatheca of IX; **C**, left spermatheca of IX.

[After Jamieson and Dyne 1976]

receiving the ampulla, discharging by a minute duct, and almost sessile; length left spermatheca of IX 0.92 mm; ratio length : length duct = 1.9; ratio length : length diverticulum = 0.3.

### Remarks

The combination of the configuration of the genital field with restriction of seminal vesicles to XII (despite the holandric condition) is distinctive of *Diploptrema intermedia*.

### *Diploptrema mantoni* Jamieson and Dyne, 1976

(Figs 101J, 106, 107)

*Diploptrema mantoni* Jamieson and Dyne, 1976: 458–459, figs 1, 3b, 9d, 10c,f, 18–20, table 1.

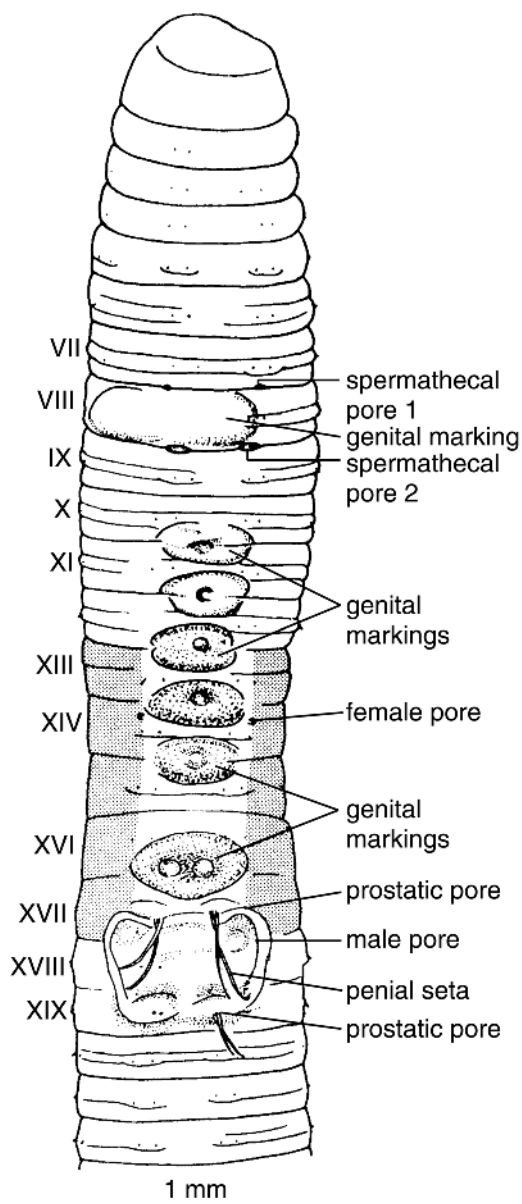
**TYPE LOCALITY:** NT, 12°50'S 131°08'E, beside Manton River, 67 km S of Darwin.

**HOLOTYPE:** QM G8400.

**PARATYPES:** QM G8401, QM G222931 (previously BJ.1975.3), AM W6605.

### Description (after Jamieson and Dyne 1976)

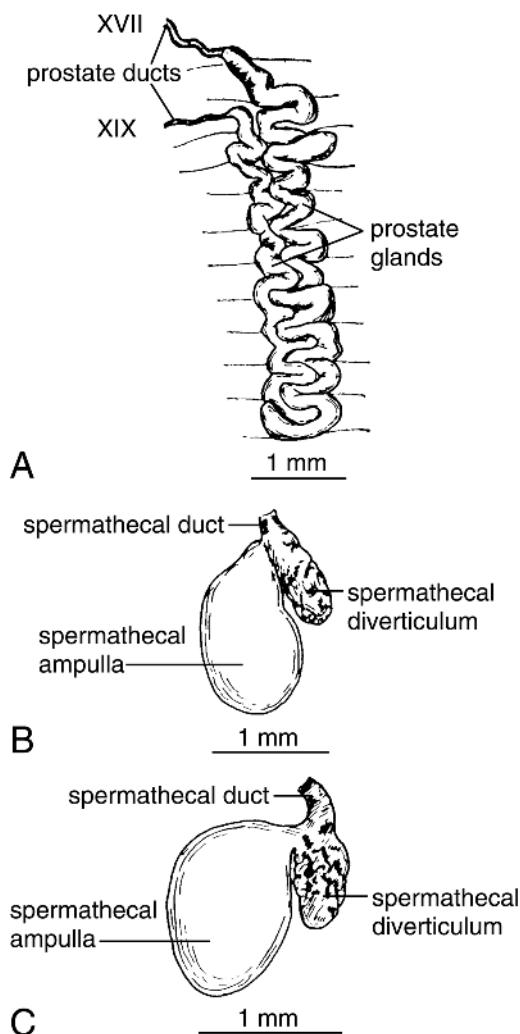
Length 39–40 mm. Width (midclitellar) 1.9–2.0 mm. Segments 99–110. Epilobous 1/3–1/2, closed, strongly convergent posteriorly. First dorsal pore 7/8 or 8/9. Genital setae in VIII. In XII,  $aa: ab: bc: cd: dd = 3.5: 1.0: 4.3: 1.0: 19.8$ ;  $dd: u = 0.55$ . Nephropores visible on the clitellum, a distance  $cd$  above  $d$ . Clitellum saddle-shaped, with ventral margins in  $b$  lines or annular, though weak ventrally. Prostatic pores on fairly large, transversely elliptical papillae, slightly median of  $a$  lines; seminal grooves narrow and distinctly visible, convex laterally but further apart at 17/18 than at 18/19, slightly indented at the minute male pores which lie shortly anterior to and a distance  $ab$  lateral of setae  $b$  of XVIII; prostatic pores of XVII 0.49 mm, 0.08 body circumference apart. The following genital markings are constant in the three type-specimens: unpaired midventral elliptical intersegmental prominences reaching the setal annulus of the preceding and succeeding segments, extending into  $ab$  laterally and with single pore-like centres, in 11/12, 12/13, 13/14 and 14/15; a larger intersegmental marking with a pair of pore-like areas in 16/17. Other, variable, markings are: an unpaired, midventral circular marking with pore-like centre presetally or postsetally in VIII; an intersegmental marking in 10/11; a transversely aligned pair of pore-like areas median to  $a$  lines posteriorly in XVII and a midventral unpaired pore-like marking anteriorly in XIX. Tumescence associated with genital setae is present bilaterally and medially conjoined or unilateral, in VIII. Female pores almost



**Fig. 106.** *Diploptrema mantoni* Jamieson and Dyne, 1976, genital field of Holotype.

[After Jamieson and Dyne 1976]

imperceptibly lateral of  $b$  lines, midway between the setal arc and anterior margin of XIV. Spermathecal pores in  $a$  lines or very slightly median to these; each a small circular orifice with a lateral, but no median bounding lip; the posterior pair 0.61 mm, 0.10 body circumference apart.



**Fig. 107, *Diploptrema mantoni* Jamieson and Dyne, 1976:**  
**A**, right prostates of Holotype; **B**, left spermatheca of IX, Holotype; **C**, left spermatheca of IX, Paratype 1.  
 [After Jamieson and Dyne 1976]

Thickest septa 6/7–9/10, moderately strongly thickened. Supra-oesophageal vessel in VII–XIII, weakly developed in XII and XIII. Last hearts in XIII; latero-oesophageal in X–XIII; dorsoventral commissurals in VI–IX. Gizzard large and cylindrical, though compressible, in V. Oesophagus in VII–XIII segmentally swollen and vascularised, with low internal rugae; narrow and whitish in XIV. Intestinal origin XV; typhlosome a small ridge, commencing in XXIII but with a trace further anteriorly. Nephridia simple throughout, commencing in II; the ducts entering the parietes

far laterally of *d* lines; preseptal funnels moderate sized, demonstrated in the anterior intestinal region. Strongly iridescent sperm funnels in X and XI; seminal vesicles 1 racemose pair, in XII. Prostate ducts in XVII and XIX; glands long, tubular, winding posteriorly into XXVIII; the bends of the two glands of a side closely interdigitating; the external ducts exceptionally slender and weakly muscularised, gradually and only slightly widening towards the body wall; the anterior glands significantly the longer. Vas deferens inconspicuous, not appearing double, on each side. Penial setae with separate *a* and *b* follicles, forming conspicuous but not especially long arcs extending through 2 segments; the setae with stout, gently curving shafts, often strongly bent ectally; apical tenth ornamented with very long, conspicuously projecting spines, highly distinctive of the species; length of mature seta 1.70 mm; midshaft diameter 22  $\mu$ m. Genital setae lacking intracoelomic glands; length of mature seta 1.36 mm, midshaft diameter 16  $\mu$ m. Ovaries flattened, with many egg strings; ovisacs absent. Spermathecae in IX significantly, though not greatly, larger than those in VIII; ampulla large, ellipsoidal, joined by a short stalk to the ectal duct where this is joined by a clavate diverticulum which has innumerable small iridescent sperm chambers in its walls; the diverticulum appearing continuous with the ectal duct whereas the stalked ampulla appears a median appendage; length right spermatheca of IX 1.8 mm; ratio total length: length duct = 3.1; ratio length: length diverticulum = 1.6.

#### Remarks

The shortly clavate spermathecal diverticulum in conjunction with the disposition of genital markings distinguishes *D. mantoni* from others in the genus.

#### *Diploptrema melaleuca* Jamieson and Dyne, 1976

(Figs 101K, 108, 109)

*Diploptrema melaleuca* Jamieson and Dyne, 1976, 459–461, figs 1, 4b, 9f, 10g, 21, table 1 -(1,2,3).

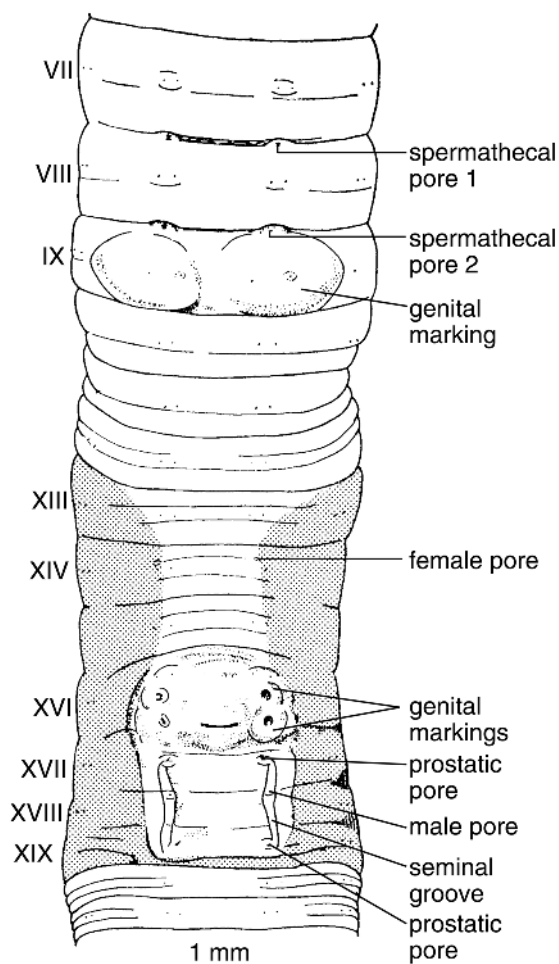
**TYPE LOCALITY:** (1) NT, 11°24'S 130°26'E, Garden Point, Melville Island.

**PARATYPE LOCALITIES:** (2) NT, 11°21'S 130°26'E, 3 km N. of Garden Point (3) NT, 11°22'S 130°26'E, 1.5 km N of Garden Point.

**HOLOTYPE:** (1) QM G8402.

**PARATYPES:** (1) QM G8403–8405, AM W6606; (2) QM G8408, 8409; (3) QM G8406, 8407.





**Fig. 108.** *Diploptrema melaleuca* Jamieson and Dyne, 1976, genital field of Holotype.

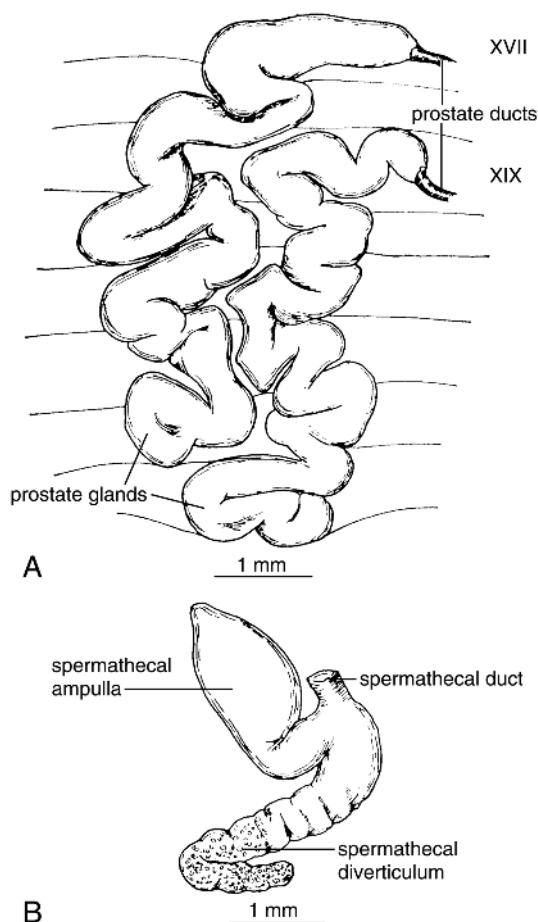
[After Jamieson and Dyne 1976]

#### **Description (after Jamieson and Dyne 1976)**

Length 212–216 mm. Width (midclitellar) 4.9–6.0 mm. Segments 297–339. Epilobous 1/3, closed, strongly convergent posteriad; peristomium with many longitudinal grooves. First dorsal pore 9/10, 10/11. Setae *a* and *b* in VIII or IX modified as genital setae. In XII, *aa*: *ab*: *bc*: *cd*: *dd* = 6.1: 1.0: 6.8: 0.9: 3.29; *dd*: *u* = 0.63. Nephropores visible on the clitellum, a straight row near the middorsal line anteriorly in their segments. Clitellum saddle-shaped, XIII–XIX, margins in *ab*. Prostatic pores minute equatorial transverse slits in *a* lines immediately median to the protruding penial setae, on elliptical mounds which constitute indistinct porophores. Male pores minute transverse slits near the anterior margin of XVIII, in *ab* nearer *b*;

seminal grooves very narrow but distinct with tumid lateral margin, leaving the lateral aspects of the prostatic porophores and therefore curving medianwards to meet the male pores although the latter are slightly lateral of the prostatic pores; prostatic pores of XVII 2.0 mm, 0.08 body circumference apart. Genital markings: a pair of postsetal circular pore-like markings in XVI and a further pair behind these in 16/17 in most specimens; a midventral transverse groove with tumid margins which may or may not be broken up into a row of shorter slits or 'pores' between the posterior pair of markings, constant in 16/17; and usually with a transversely elliptical pad at intersegment 21/22 with, at fullest development, a median and 2 lateral 'pores'. Ventral tumescences usually surround genital setae on IX and occur less commonly in VIII. Female pores a pair, shortly anterior to *ab* of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *ab*, on small papillae.

Thickest septa 8/9–10/11, moderately strongly thickened. Supra-oesophageal in VII–½XIV. Last hearts in XIII, latero-oesophageal in X–XIII; dorsoventral commissurs in VI–IX also valvular. Gizzard large, cylindrical with anterior rim, strongly muscular but slightly compressible in V, oesophagus in VII–XIV wide, narrowing intersegmentally, vascularised, internally rugose. Intestinal origin XVI; well-developed dorsal typhlosome present from XXV. Nephridia first visible in III where they are small though considerably coiled; in IV–VII forming very large tufts with many spiral loops; those in V and VII exonephric with ducts entering the parietes well lateral of *d* lines as do those of the unmodified nephridia; those of IV with the duct, on each side, running to the pharynx and probably enteronephric; preseptal nephrostomes demonstrated in the anterior intestinal region. Large iridescent free sperm funnels in X and XI; seminal vesicles 2 pairs, racemose with numerous large conspicuous loculi, in XI and XII, the posterior pair slightly the larger. Prostates flattened, much coiled tubes extending posteriorly into segment XXIV; the ectal duct long and very slender. Vas deferentia not seen. Penial setae with separate *a* and *b* follicles forming conspicuous arcs extending into XX, an extensive median glandular mass (associated with the genital field) lies under and lateral to the nerve cord in XVI–XX, into which the long prostatic ducts and penial setae pass before entering the body wall. Penial setae: long thin and tapering; ornamented with numerous prominent teeth (usually solitary, but also in bracts of 2–3) at an angle to the shaft, on the distal tenth; length of mature seta 5.65 mm; midshaft diameter 23 µm. Large follicles but no intracoelomic glands



**Fig. 109.** *Diploptrema melaleucae* Jamieson and Dyne, 1976, Holotype: **A**, left prostates; **B**, left spermatheca of IX. [After Jamieson and Dyne 1976]

### Remarks

The genital field and the unusually long spermathecal diverticulum are distinctive of *Diploptrema melaleucae*.

### *Diploptrema minuta* Jamieson and Dyne, 1976

(Figs 101L, 110, 111)

*Diploptrema minuta* Jamieson and Dyne, 1976: 461–462, figs 1, 2a, 9e, 10h, 22, table 1.

**TYPE LOCALITY:** NT, 12°25'S 130°51'E, Bagot Road, Darwin.

**HOLOTYPE:** QM G8410.

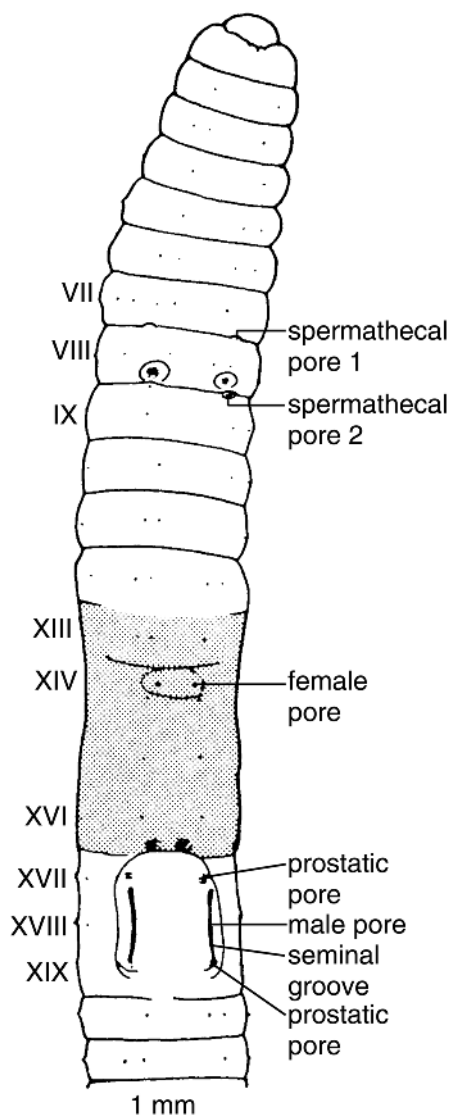
**PARATYPES:** QM G8411, 8421 (re-registration), AM W6607.

### Description (after Jamieson and Dyne 1976)

Length 21–26 mm. Width (midclitellar) 1.0 mm. Segments 78–84. Epilobous 1/2 open, almost parallel-sided. Genital setae absent. In XII,  $aa: ab: bc: cd: dd = 3.2: 1.0: 2.1: 1.4: 13.7$ ;  $dd: u = 0.53$ , but  $cd$  diverging posteriorly so that caudally this interval is almost as wide as  $bc$ . First dorsal pore 7/8. Nephropores not externally recognisable. Clitellum annular, XIII–XVI, ½XVII. Prostatic pores minute, in  $ab$ , not on appreciable porophores; seminal grooves narrow, distinctly developed and almost straight but slightly convergent towards the equator of XVIII; male pores not certainly recognisable but apparently minute points in the seminal grooves equatorially in  $a$  lines in XVIII; prostatic pores of XVII 0.26 mm, 0.08 body circumference apart. Genital markings usually absent or a circular marking with a pore-like centre paired in  $ab$  postsetally in VIII or paired median to  $a$  posteriorly in XVI. No ventral tumescence in the vicinity of the spermathecal segments apart from the postsetal genital marking in VIII. Female pores minute, in or very slightly median of  $a$  lines midway between the setal arc and anterior margin of XIV, in a common elliptical field. Spermathecal pores in  $b$  lines on minute papillae, the posterior pair (H) 0.48 mm, 0.15 body circumference apart.

Septa 8/9 and 9/10 the thickest, moderately strongly thickened. Supra-oesophageal vessel in ½IX–XIII; last hearts in XII; latero-oesophageal in X–XII, though only supra-oesophageal connectives certainly recognisable; dorsoventral commissurals in VIII and IX (and further anteriorly?). Gizzard relatively large, barrel-shaped, strongly muscular though compressible, in V; septum 5/6 exceedingly delicate and ensheathing it. Oesophagus in VIII–XII segmentally dilated and vascularised but lacking calciferous glands; narrow and less vascular in

associated with the genital setae of VIII and IX; length of mature seta 1.75 mm; midshaft diameter 37  $\mu$ m. Ovaries large sheaves of oocytic strings; no ovisacs demonstrable. Spermathecae elongate ovoid and apically pointed, restricted to the segment of their ducts or reflexed anteriorly through 1 or 2 segments; with a short slender duct which is joined ectally by a diverticulum which begins as a wide tube and elongates to form a long coiled blind tube the ectal half of which is iridescent owing to innumerable minute spherical seminal chambers in its walls; length of left spermatheca of IX 4.4 mm; ratio of length spermatheca: length of duct = 8.7; ratio of length: length of diverticulum = 1.2.



**Fig. 110.** *Diploptrema minuta* Jamieson and Dyne, 1976, genital field of Holotype.

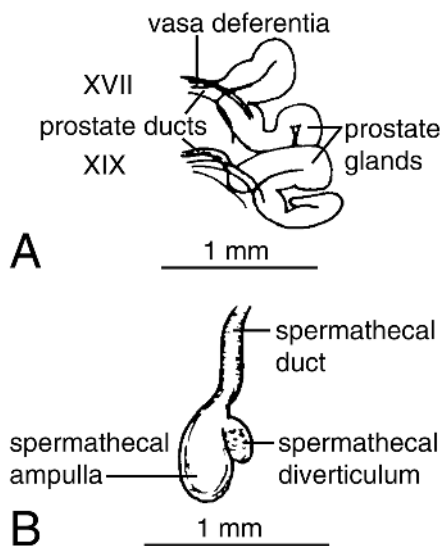
[After Jamieson and Dyne 1976]

XIII. Intestinal origin XIV, a well-developed broadly laminar dorsal typhlosole commencing in XVI. Nephridia simple throughout, commencing in II; preseptal funnel demonstrated in the mid-intestinal region. In some post-prostatic segments there are 2 stomate nephridia on each side, the duct of the median and lateral nephridium entering the parietes in *b* line, and far lateral of *d* line, respectively. Iridescent free sperm funnels in X and XI; 1 pair of large sacciform seminal vesicles in XII. Prostates with the tubular glands

each bent several times on itself and occupying 2 or 3 segments, the ectal duct very slender and slightly tortuous. Vasa deferentia not recognisable. Penial setae with separate *a* and *b* follicles, forming conspicuous arcs, almost reaching the posterior end of the corresponding prostate; the setae small and very thin with very few scattered and inconspicuous blunt teeth (usually in groups of 2) on the distal third; length of a mature seta 0.77 mm; midshaft diameter 11  $\mu$ m. Ovaries small with few egg strings; several large loculi on the anterior septum of XIV are apparently ovisacs. Spermathecae uniform in size; each with an ovoid ampulla, long bent or tortuous slender, well-differentiated duct and subspherical highly iridescent diverticulum. The diverticulum almost sessile at the junction of ampulla and duct, with very numerous spheroidal sperm chambers in its walls; length of the right spermatheca of IX 1.1 mm; ratio of total length: length duct = 2.0; ratio of length: length diverticulum = 4.9.

#### Remarks

Intestinal origin, in *Diploptrema minuta*, in XIV is the most anterior known in the Megascolecidae other than the Ocnerodrilinae in which it is in segment XII or XIII. A short oesophagus is unquestionably a primitive (plesiomorphic) character; location of last hearts in *D. minuta* in XII rather than XIII is also plesiomorphic. If these conditions were primitive in *D. minuta* and not a secondary regression associated with reduction in



**Fig. 111.** *Diploptrema minuta* Jamieson and Dyne, 1976, Holotype: **A**, right prostates; **B**, right spermatheca of IX.  
[After Jamieson and Dyne 1976]

body size, Australian acanthodrilids would have to be considered very primitive representatives of the Acanthodrilinae. Replication of some holonephridia is an apomorph character rare in the Acanthodrilinae, however, and demands caution in regarding the apparent plesiomorph characters of *D. minuta* as primitive. It is presumed that the absence of genital setae is a regression in this species. The partial duplication of nephridia is an approach to the meroenephric condition of *Neodiploptrema*.

***Diploptrema planumfluvialis* Dyne, 1987**

(Figs 112, 113, 126A-C)

*Diploptrema planumfluvialis* Dyne, 1987: 1–3, figs 1–2, 4–6.

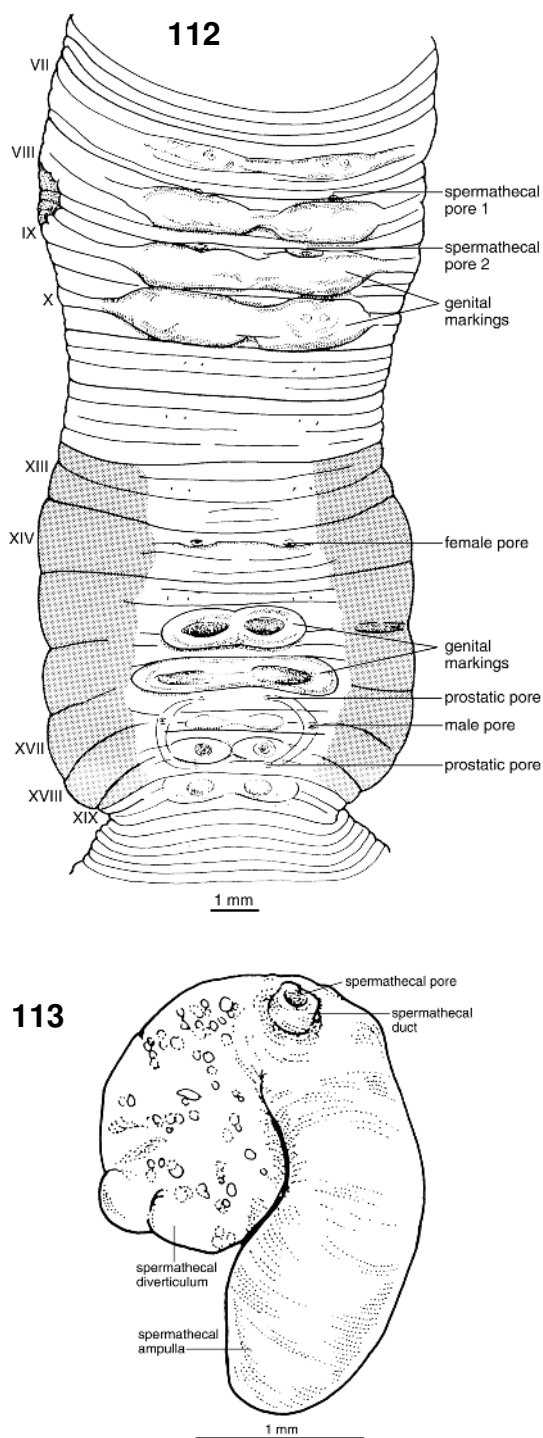
**TYPE LOCALITY:** NT, 13° 05'S 131° 14'E, Upper Adelaide River Experimental Station, Adelaide River Floodplain, solodic soil. Coll. B. Wood, 8 Mar 1984.

**HOLOTYPE:** NTM Wo1.

**PARATYPE:** NTM Wo2–5

**Description (after Dyne 1987)**

Length 192, 145 mm. Width 8.6, 6.4 mm. Segments 255–266. Whitish-grey in alcohol, clitellum orange-pink. Prostomium pro-epilobous, peristomium longitudinally creased. First perforate dorsal pore 11/12. Setae in regular rows throughout, ventral setal pairs lacking in XVIII, modified as penial setae in XVII and XIX; in XII, *aa: ab: bc: cd: dd* = 10.1: 1.9: 17.4: 1.4: 48.86. Penial setae present, genital setae lacking. Nephropores not externally recognisable. Clitellum saddle-shaped, skirting the ventrum well lateral of *b* lines, extending from mid-XII (weak) to mid-XIX; thickly tumid, obscuring all other external features save the intersegmental furrows. Male pores seen as minute orifices, lateral of *b* lines, at 17/18 just medially to the edge of a pair of broad, shallow seminal grooves that link the porophores. The latter are poorly defined, ?coincident with *b* setae, and scarcely elevated, on minute papillae. Genital markings four conspicuous, broad tumid bands almost cover the ventral surface of segments VII–X, the anteriormost marking the least well developed, those on VIII and IX subequal, that on X the most extensive (all mature specimens). Though these markings resemble the tumescences associated with genital seta follicles in other species, such follicles are lacking. Segment IV has a glandular appearance in the holotype, with a well-developed bipartite marking present in 14/15 in P1. A pair of oculate markings (elevated rims surrounding a circular concave area) present intersegmentally in



**Figs 112, 113, *Diploptrema planumfluvialis* Dyne, 1987, Holotype. 112, genital field; 113, right spermatheca of IX.**  
[After Dyne 1987]

15/16 (sometimes a single, midventral marking) and in 16/17, where the eyelike markings are more widely separated than in the latter intersegment, on all mature specimens. Ill-defined glandular markings in 17/18 and 19/20 (all specimens). Small, closely paired oculate markings also present in 19/20 in all mature specimens. Intersegment 20/21 sometimes with a single, midventral oculate marking. Female pores somewhat disguised by the development of glandular tumescence in XIV, located presetally in mid *ab*. Small spermathecal pores, hidden by tumid pads, present in *a* lines in 7/8, 8/9.

Septa 5/6–6/7 moderately thickened, 7/8–9/10 fairly strongly muscularised, 8/9 perhaps the thickest, 10/11–11/12 moderately thickened, remainder thin. Dorsal blood vessel single, traceable anteriorly to the pharynx; last hearts in XIII. A supra-oesophageal vessel is present in VIII–XIV. In X–XIII, the commissurals appear to communicate only with the supra-oesophageal vessel, but with the anterior diminution of the latter, the connectives (from IX anteriorly) become associated with the dorsal vessel. Gizzard moderately developed, globose and readily compressed, in V. Oesophagus broad and vascular, particularly in posteriormost section, but narrowing immediately before commencement of intestine, in XVIII. No distinct calciferous glands present. Typhlosole absent. Ingesta: soil particles only (no recognisable organic remains). Small to medium-sized iridescent spermatic funnels present in X and XI, and large acinous seminal vesicles present in XI and XII. Prostate glands consist of a tubular, compactly coiled glandular portion, restricted to segment of origin, or, in the case of the anterior organs only, rarely extending partially into the succeeding segment; anterior prostatic pairs are more than twice the size of the posterior organs. Prostatic ducts short and non-muscular. Penial seta follicles contain several setae, some reddish in appearance, associated with the prostatic ducts. Setae gently curving, ornamented over the distal half with regularly arranged depressions, which appear as jagged excavations, and approximately 2 mm in length when mature. Ovaries consist of delicate, flattened webs of connective tissue with embedded oocytes; these and medium-sized iridescent oviducal funnels present in XIII, ovisacs absent. Spermathecae 2 pairs, each composed of a short duct, tubulodigitiform ampulla, and sessile, sacciform diverticulum, the latter filled with numerous iridescent sperm locules. Length of right IX spermatheca 3.1 mm. Genital setae or associated glands absent.

## Remarks

*Diploptrema planumfluvialis* has affinities with the widespread *D. shandi*, agreeing in the overall construction of the spermathecae, ornamentation of the penial setae, position of the seminal vesicles, and arrangement of the blood vascular system. *D. planumfluvialis* is distinctive, however, in having the prostate glands almost always restricted to their segments or origin, an abbreviated condition, which elsewhere in the Northern Territory is only seen in two very small species. The appearance of the genital field is also diagnostic.

The worms produce large columnar cast accumulations up to 25 cm in height and 12 cm in diameter (B. Wood, pers. comm.), rivalling the largest recorded in the Oligochaeta. Extensive surface casting is also known for *D. heteropora* Dyne in the Townsville region (A.V. Spain, pers. comm.) Dyne (1979a) noted that the latter species was also geophagous and apparently adapted to a wet/dry climatic regime. Lee (1967) reported on the adaptive exploitation of soil microrelief for wet season survival by the large surface casting earthworm, *Pheretima tumulifaciens*, in New Guinea, but this phenomenon has not been investigated in the Acanthodrilinae. The ability of *D. planumfluvialis* to survive a floodplain habitat with a monsoonal climatic regime may be at least partially due to its geophagous, rather than phytophagous, dietary mode and an amphibious propensity, a feature shared by a number of its eastern Australian congeners (Dyne 1987).

## *Diploptrema ridei* Jamieson and Dyne, 1976

*Diploptrema ridei* Jamieson and Dyne, 1976: 462–467, figs 1, 5a,b, 6, 9g,h, 10i,j, 23–30, table 2. For records, see subspecies.

## Description (after Jamieson and Dyne 1976)

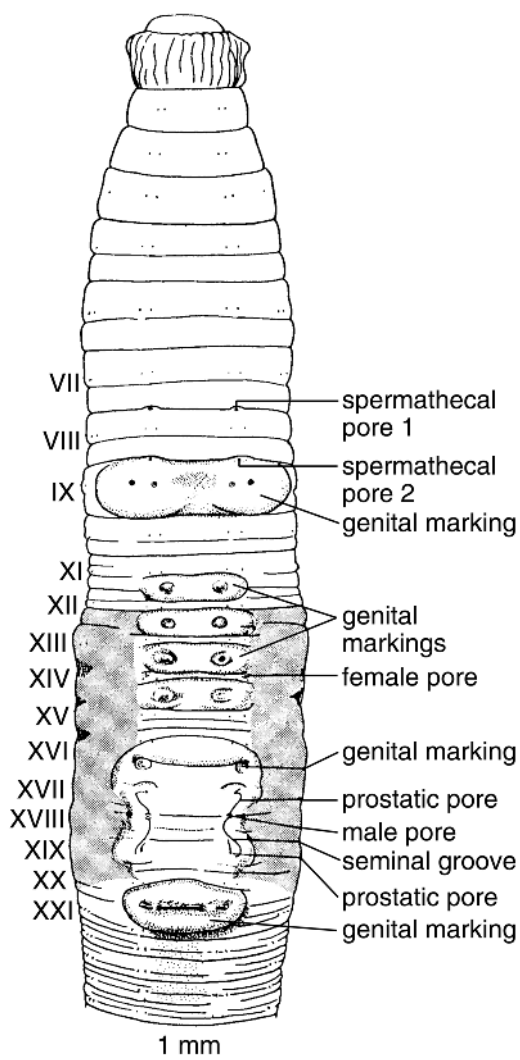
Length 82–195 mm. Width (midclitellar) 4.2–4.7 mm. Segments 226–314. Prolobous or slightly pro-epilobous. Peristomium with many longitudinal grooves. First dorsal pore 10/11. Genital setae in IX or VIII and IX. Nephropores slightly nearer the middorsal line than *d* line. Clitellum XIII–2/3XX, XX, saddle-shaped with margins in *ab* or annular but weakly developed ventrally. Prostatic pores in *ab*; male pores (always?) at the anterior margin of XVIII slightly median of *a* lines. Seminal grooves almost straight or convex medially. Prostatic pores of XVII 0.7–1.9 mm, 0.06–0.12 body circumference apart. Genital markings: intersegmental pads constant in 12/13, 13/14 and 16/17; usually in 11/12 and 14/15, less frequently in 10/11 and 21/22 (both subspecies); frequently in the nominate subspecies in 20/21 and

less often in 19/20; commonly in *melvillensis* in 15/16, 22/23, 23/24 and less frequently 24/25. Female pores shortly presetal in *ab* or *b*. Spermathecal pores in *ab* on small protuberances; the posterior pair 1.1–1.7 mm, 0.09–0.13 body circumference apart.

Thickest septa 5/6, 6/7–10/11 strongly thickened. Supra-oesophageal vessel in VII, IX–XIV. Last hearts in XIII; latero-oesophageal in X–XIII; dorsoventral commissurals in VI–IX, also valvular. Gizzard large, strongly muscular though compressible, broadly fusiform restricted to V but with transverse encircling rim, sometimes poorly defined, suggestive of duplication. Oesophagus in VII, VIII–XV, XVI, segmentally dilated and vascularised but lacking calciferous glands; slender and chloragogenous-looking in XVI or XVII. Intestinal origin in XVII or XVIII respectively, a broad but distinct low dorsal typhlosole commencing in the region of XXV–XXX. Nephridia small in II and III; forming a pair of very large tufts in each of IV and V of which at least those in V send a duct forward on each side to join the buccal cavity dorsolaterally anterior to the brain; slightly smaller tufts in VI apparently exonephric in this segment; succeeding nephridia simple stomate avesculate exonephric holonephridia, each with a single preseptal funnel (funnels demonstrated in anterior intestinal region); ducts entering the parietes nearer the middorsal line than *d* line. Iridescent free sperm funnels in X and XI; seminal vesicles large, compactly racemose, subequal pairs in XI and XII. Prostates tubular, tortuous or almost straight; extending into approximately XXIV–XXVII; the anterior pair significantly the longer; ectal ducts slender but fairly short entering intracoelomic parietal glands corresponding with the porophores. Penial setae in conspicuous follicles extending to or beyond the corresponding prostate glands and closely adherent to them; *a* and *b* follicles not separate; the setae with bracts of denticles scattered or in circlets, usually with larger solitary spines or teeth; length 6–10 mm. Genital setae in IX or VIII and IX, with large follicles but no intracoelomic glands, setal length 1.3–1.7 mm. Ovaries with several to many egg strings; multiloculate ovisacs present. Spermathecae 2 subequal pairs; ampulla ovoid, with moderately slender stalk; diverticulum elongate tongue-shaped, almost sessile on the body wall so that the stalked ampulla appears to be an appendage; the diverticulum with several to many large externally protuberant intramural seminal chambers; length of a posterior spermatheca 1.7–1.9 mm; ratio length spermatheca: length duct = 2.8–4.7; ratio of length: length of diverticulum = 0.7–0.9.

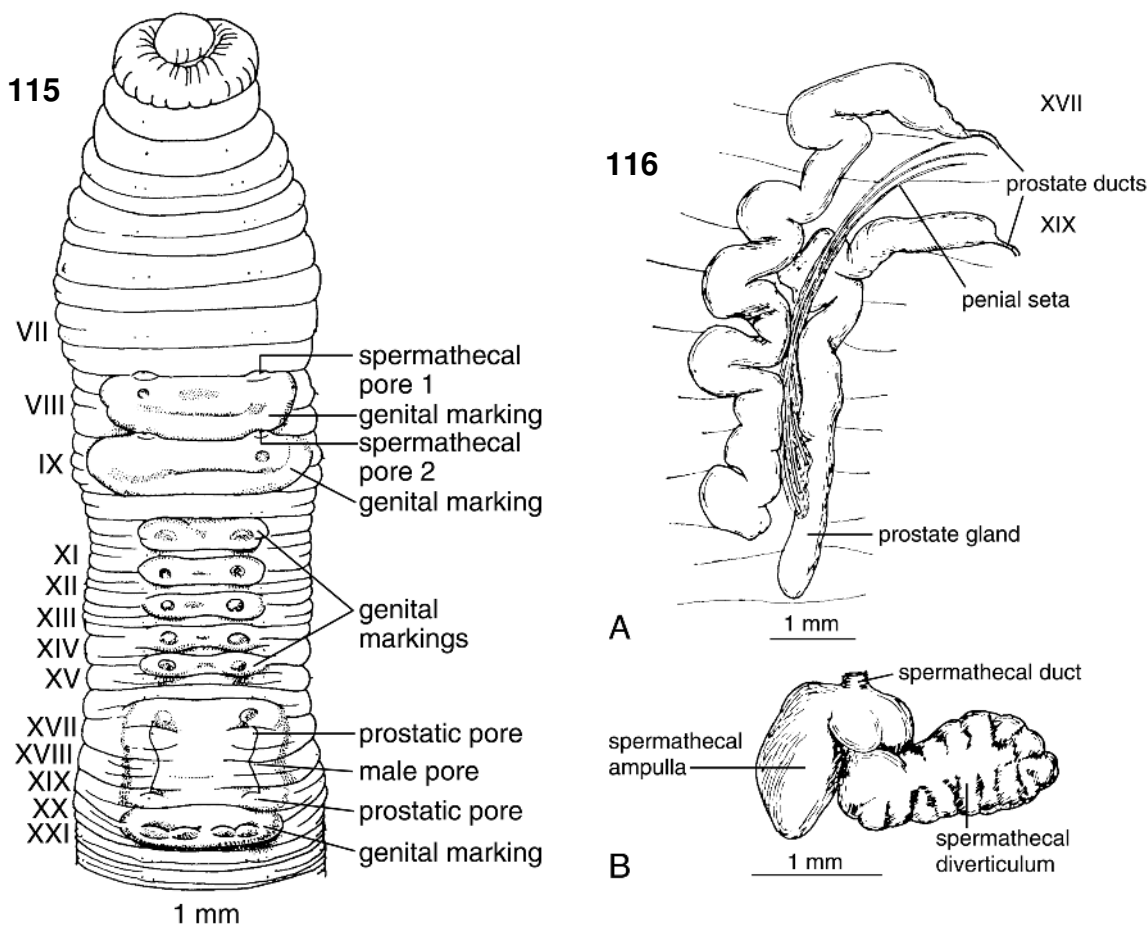
### Remarks

Both subspecies of *D. ridei* are distinguished from all other species of the genus by the depressed tongue-like spermathecal diverticulum with bordering seminal chambers. The Melville Island subspecies differs from the nominate, mainland, subspecies in usually possessing an accessory genital marking in 15/16 which has not been observed in the latter. Frequent location of posterior genital markings in 19/20 and 20/21 in *D. r. ridei* also contrasts with that in 22/23–24/25 in *D. r. melvillensis*.



**Fig. 114.** *Diploptrema ridei ridei* Jamieson and Dyne, 1976, genital field of Holotype.

[After Jamieson and Dyne 1976]



Figs 115, 116, *Diploptrema ridei ridei* Jamieson and Dyne, 1976. 115, genital field of Paratype 8; 116, Holotype: A, left prostates; B, left spermatheca of VIII. [After Jamieson and Dyne 1976]

***Diploptrema ridei ridei* Jamieson  
and Dyne, 1976**

(Figs 114–116, 119A–C)

*Diploptrema ridei ridei* Jamieson and Dyne, 1976: 464–467, figs 1, 5a,b, 9g, 10i, 23–25, table 2.

**TYPE LOCALITY:** (1) NT, 12.48°S 131°27'E, 3 km W of Leaning Tree Billabong near Humpty Doo.

**PARATYPE LOCALITIES:** (1) As above. (2) NT, 12.27°S 131°07'E, 7 km NE of Howard Springs. (3) NT, 12°41'S 131°25'E, eastern edge of Buffalo Plains, E of Humpty Doo. (4) NT, 12°46'S 131°29'E, 7 km E of Leaning Tree Billabong.

**HOLOTYPE:** QM G8413.

**PARATYPES:** (1) QM G8414–8417, QM G222932 (previously BJ.1975.7.6), AM W6608, 6609; (2) QM G8421; (3) QM G8418–8420; (4) QM G8422.

**Description (after Jamieson and Dyne 1976)**

Length 82–102 mm. Width (midclitellar) 4.2–4.4 mm. Segments 226–232. In XII,  $aa:ab:bc:cd:dd = 6.0:1.0:5.6:0.8:33.3$ ;  $dd:u = 0.62$ . Proepilobous. Setal lines regular throughout. Nephropores faintly visible on the clitellum slightly nearer the middorsal line than  $d$  line. Clitellum XIII– $\frac{1}{3}$ XX, XX, saddle-shaped with margins in  $ab$ , or annular but weakly developed ventrally. Prostatic pores in  $ab$  nearer  $a$ ; male pores minute transverse slits at the anterior margin of XVIII, slightly median of  $a$  lines; seminal grooves narrow and distinctly visible, curving from the lateral aspects of the prostatic pores towards the ventral midline in XVIII, including the male pores but reaching their most median position at the equator of XVIII considerably behind the male pores; prostatic pores of XVII 1.7 mm,

0.12 body circumference apart. Genital markings: a midventral transverse intersegmental pad usually extending shortly lateral of *b*, with paired 'pores' shortly median to *a* lines, in 10/11 (rarely), 11/12, 12/13, 13/14 and 14/15 (constant) sometimes with a median 'pore' also. A wider marking constant at intersegment 16/17 confluent with the male field which may show a pair or a triplet of 'pores' or may lack these but have a single concavity occupying most of its area. Most specimens with a large midventral transverse intersegmental pad in 20/21, and filling much of the lengths of each adjacent segment, bearing 3 or more transverse narrow gutters; similar but smaller pads sometimes present at 19/20 or 21/22. Epidermal tumescence constant surrounding the ventral setal couples in IX and sometimes VIII also. Female pores in *b* lines. Spermathecal pores in *ab*, nearer *b*; the posterior pair 1.7 mm, 0.13 body circumference apart.

Supra-oesophageal vessel in VII–XIV. Oesophagus dilated and vascularised in VII–XV; slender in XVI. Intestinal origin XVII, typhlosole commencing in XXV or XXVI though with a trace in the next anterior segment. Prostates depressed tubular, winding into XXIV and XXV, or XXVI and XXVII. Penial setae with elongate shafts, often sharply bent ectally; ornamentation confined to the ectal tenth and comprising scattered bracts of denticles closely adherent to the shaft and larger, usually solitary, teeth projecting at an angle to the shaft which are more numerous apically; length of mature seta 5.85 mm; midshaft diameter 15  $\mu$ m. Genital setae with concavities over the ectal half; length of mature seta 1.25 mm; midshaft diameter 26  $\mu$ m. Length left spermatheca of IX 1.9 mm, ratio length: length duct = 4.7; ratio length: length diverticulum = 0.9.

***Diploptrema ridei melvillensis* Jamieson and Dyne, 1976**

(Figs 117, 118, 119D–H)

*Diploptrema ridei melvillensis* Jamieson and Dyne, 1976: 467, figs 1, 6, 9h, 10j, 26–30; table 2

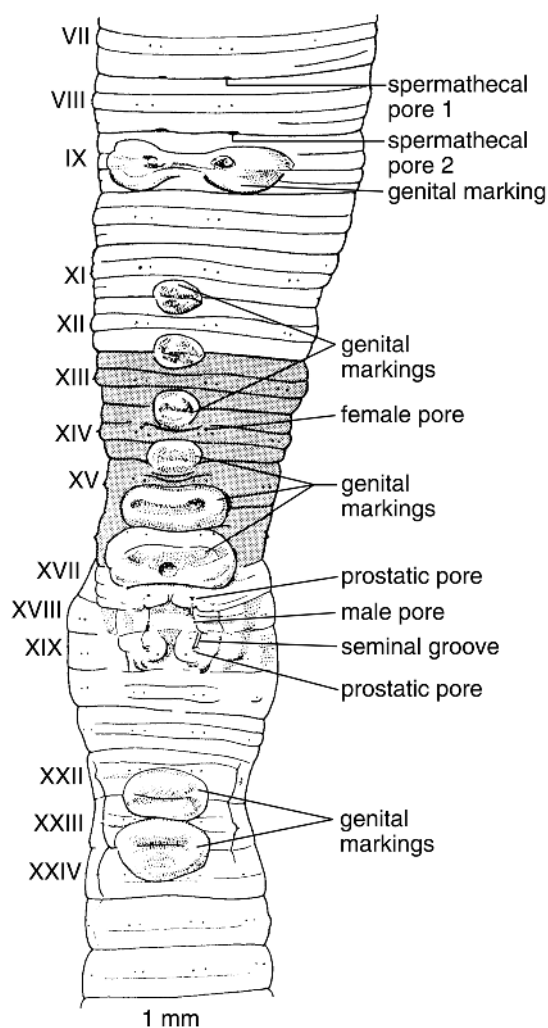
**TYPE LOCALITY:** NT, 11°25'S 130°40'E, Snake Bay, Melville Island.

**HOLOTYPE:** QM G8423.

**PARATYPES:** QM G8424, 8425, QM G222933–222934 (previously BJ.1975.7.8/9), AM W6610, 6611.

**Description (after Jamieson and Dyne 1976)**

Length 143–195 mm. Width (midclitellar) 4.7 mm. Segments 294–314. Prolobous. Some irregularity in the ventral and dorsal setal couples near the



**Fig. 117.** *Diploptrema ridei melvillensis* Jamieson and Dyne, 1976, genital field of Holotype.

[After Jamieson and Dyne 1976]

caudal extremity. In XII, *aa: ab: bc: cd: dd* = 5.2: 1.0: 6.8: 0.8: 42.3; *dd: u* 0.66. Clitellum incompletely developed. Prostatic pores in *ab*; male pores not recognisable. Seminal grooves narrow and indistinct, medially convex or almost straight; prostatic pores of XVII 0.73–1.9 mm, 0.06–0.09 body circumference apart. Genital markings, a midventral elliptical intersegmental pad median to *a*, lines with or without a pair of pores, sometimes in 10/11; usually in 11/12, constant in 12/13 and 13/14; and usually in 14/15. Frequently with a wider marking, extending lateral of *b* in 15/16 with or without a pair of 'pores' and constantly with a wider marking at 16/17 confluent



with the male field which may show a pair or triplet of pores or may have a single concavity occupying most of its area. A large midventral transverse pad at one or more of intersegments 21/22–24/25, most frequent at 23/24 and/or 24/25. Epidermal tumescence constant surrounding the ventral setal couples in IX. Female pores in *ab*. Spermathecal pores in mid *ab*; the posterior pair 1.1 mm, 0.09 body circumference apart.

Supra-oesophageal vessel traceable in IX–XIV. Oesophagus dilated and vascularised in VIII–XVI, slender in XVII. Intestinal origin XVIII; typhlosole commencing in XXVIII or XXX. Nephridia as described for species. Prostates partly tortuous but with long straight portions, not notably depressed, extending into XXVI or XXVII. Penial setae with exceedingly long, hair-like shafts, irregularly bent after removal from follicle, with circlets of jagged bracts interspersed with larger solitary spines nearest the apical region, the bracts disappearing further entally, with only large spines present; length of mature seta 9.46 mm, midshaft diameter 14  $\mu$ m. Length of mature genital seta 1.72 mm, midshaft diameter 22  $\mu$ m. Length left spermatheca of IX 1.7 mm; ratio length: length duct = 0.7; ratio length: length diverticulum = 0.7.

***Diploptrema shandi* Jamieson and Dyne, 1976**

(Figs 119I–L, 120–124)

***Diploptrema shandi*** Jamieson and Dyne, 1976: 468–471, figs 1, 7a,b, 8a,b, 9i,j, 10k–o, 31–34, table 2.

**TYPE LOCALITY:** (1) NT, 16°04'S 136°17'E, N. of Borroloola on road to Bing Bong.

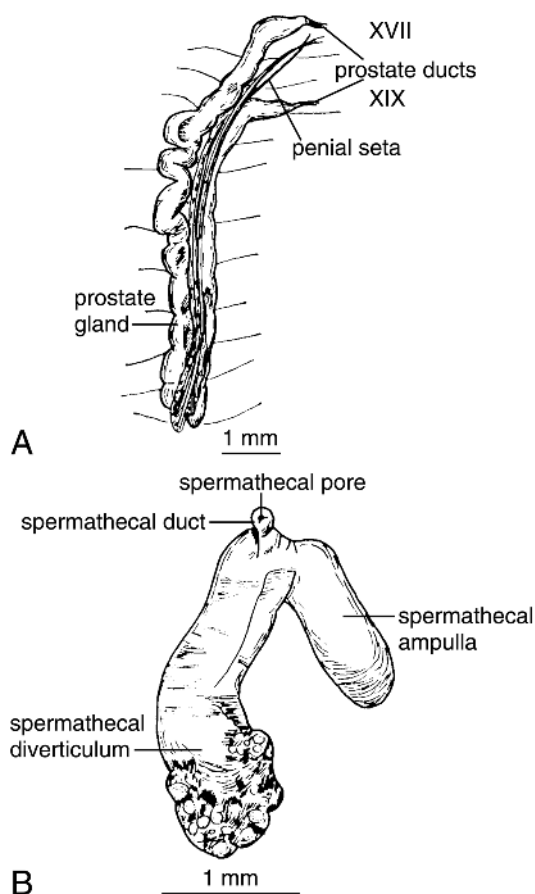
**PARATYPE LOCALITIES:** (1) As above. (2) NT, 16°08'S 136°04'E, Ryan's Bend Waterhole, SW of Borroloola. (3) NT, 12°26'S 138°08'E, 10 km NE of Howard Springs. (4) NT, 12°48'S 131°27'E, 3 km W of Leaning Tree Billabong, near Humpty Doo. (5) NT, 13°30'S 131°12'E, 150 km S of Darwin. (6) NT, 14°55'S 133°08'E, Mataranka Springs.

**HOLOTYPE:** (1) QM G8426.

**PARATYPES:** (1) QM G8427–8439, 8440–8456, AM W6612–6621; (2) QM G8457–8466, 8775–8778; (3) BJ 1975.7.35; (4) QM G8779–8781; (5) QM G8782–8789; (6) QM G8790–8794.

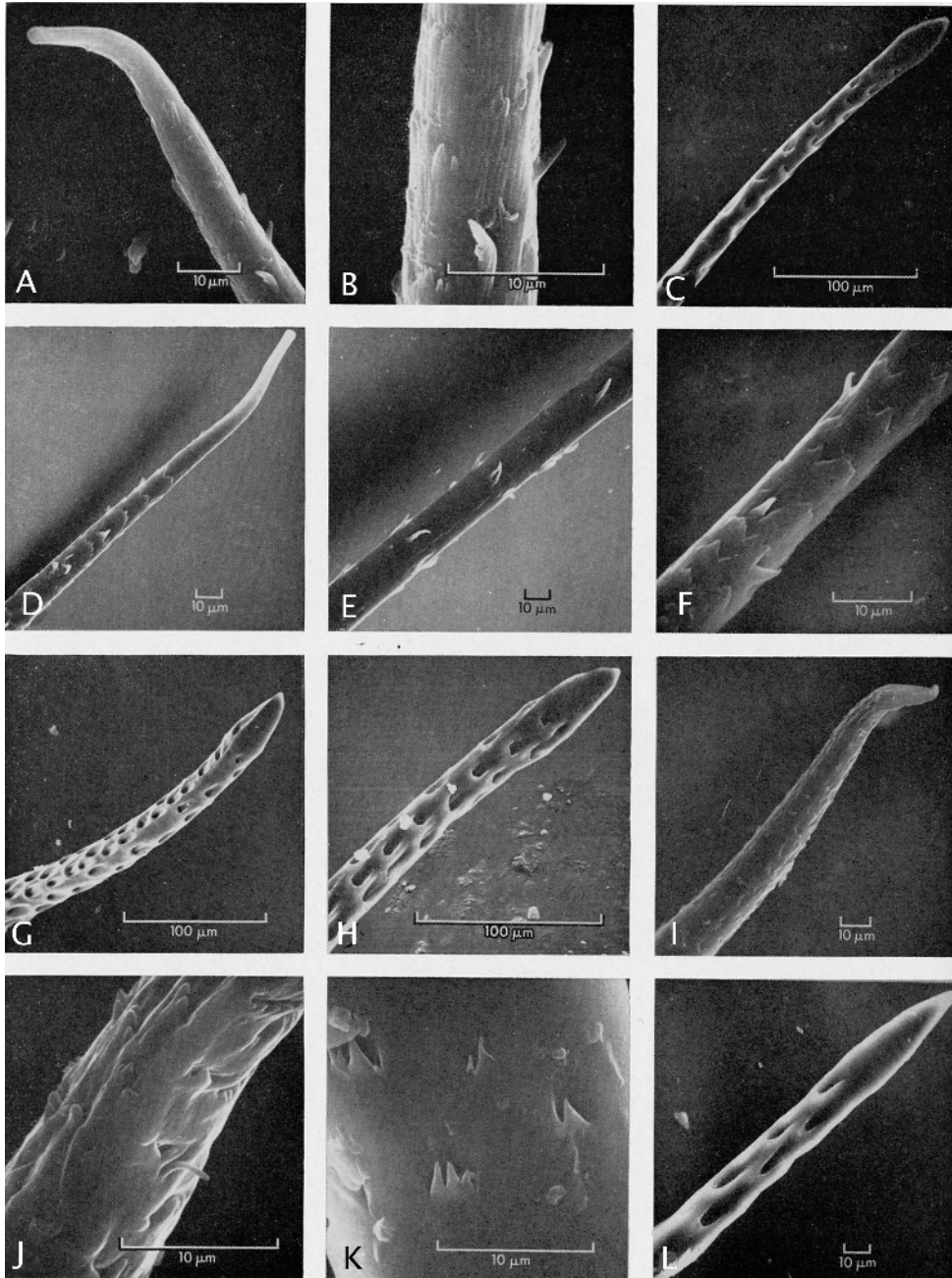
**Description (after Jamieson and Dyne 1976)**

Length 69–70 mm. Width (midclitellar) 2.6 mm. Segments 132–137. Epilobous 1/2 open or closed, narrowing posteriorly. First dorsal pore 7/8.

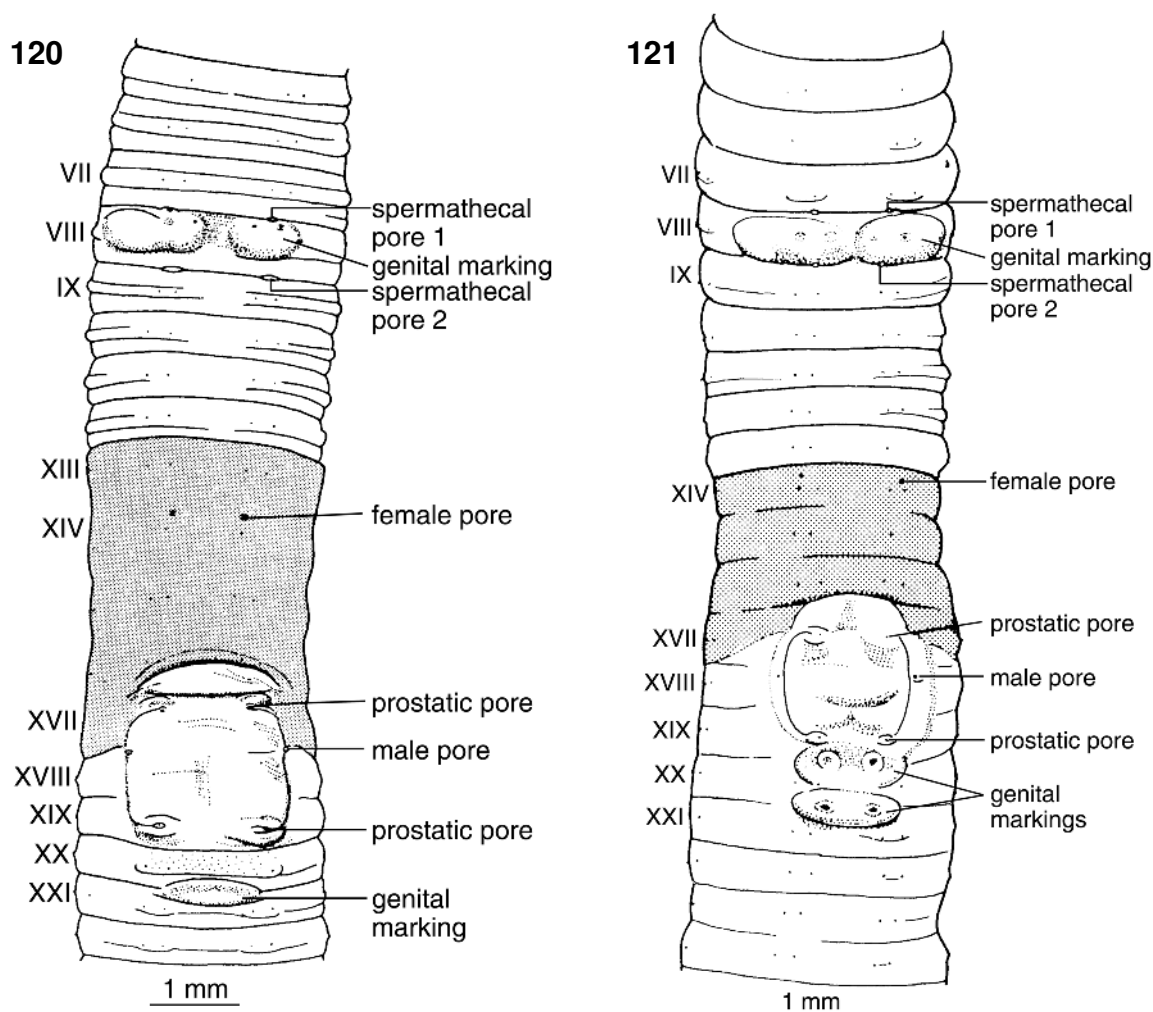


**Fig. 118.** *Diploptrema ridei melvillensis* Jamieson and Dyne, 1976, Paratype 1: **A**, left prostates; **B**, right spermatheca of VIII. [After Jamieson and Dyne 1976]

Genital setae (as judged from epidermal tumescence) in VIII and/or IX, or VII and/or VIII; all setae present in XVIII; in XII, *aa*: *ab*: *bc*: *cd*: *dd* = 3.5: 1.0: 3.9: 1.0: 15.0; *dd*: *u* = 0.49. Nephropores faintly visible on the clitellum in *d* lines. Clitellum XIII–XVII, annular excepting in XVII and posterior XVI, where it is interrupted ventrally by the male genital field. Prostatic pores in *ab* on distinctly developed transversely elliptical low porophores; male pores minute at the anterior margin of XVIII, well lateral of *b* lines; seminal grooves narrow, well developed, convex laterally, including the male pores and not greatly diverging from these to the equator of XVIII; prostatic pores of XVII 1.0 mm, 0.12 body circumference apart. The most characteristic genital markings are a midventral pad in 16/17, typically with a pair of pore-like markings approximately in *a* lines; a transverse pad, with or



**Fig. 119.** Penial and genital setae in *Diploptrema*: **A, B,** *D. ridei ridei*, penial; **C,** genital; **D-F,** *D. ridei melvillensis*, penial; **G, H,** *D. ridei melvillensis*, genital; **I-K,** *D. shandi*, penial; **L,** *D. shandi*, genital. [After Jamieson and Dyne 1976]

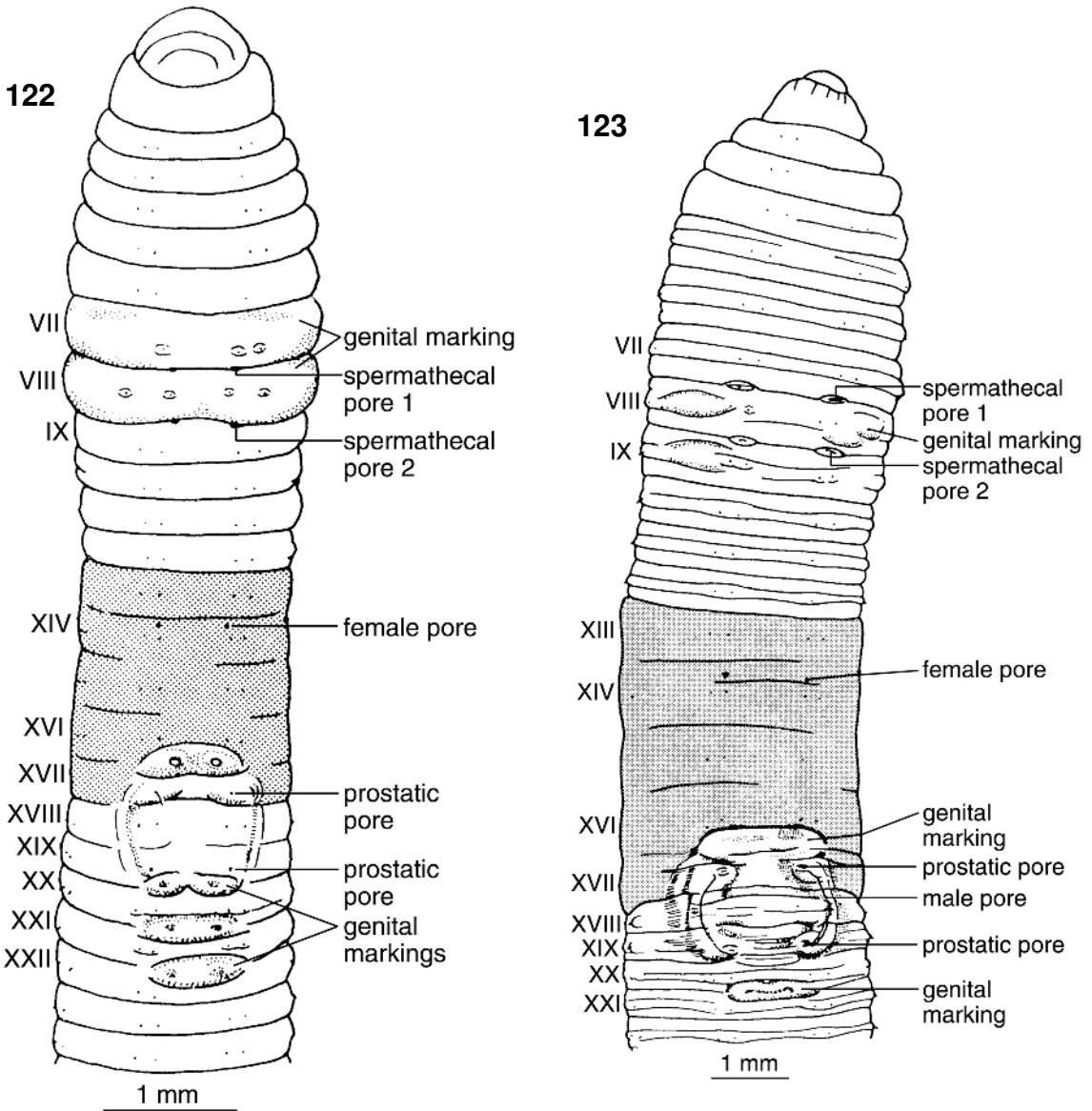


**Figs 120, 121, *Diploptrema shandi* Jamieson and Dyne, 1976. 120, genital field of Holotype; 121, genital field of Paratype 28.** [After Jamieson and Dyne 1976]

without a pair of 'pores', or a pair of markings with central pores, in 19/20; a similar pad or pair of markings in 20/21; a pad or pair of markings in 17/18; similar marking(s) in 21/22. Less common are similar markings in 18/19; rarely with markings in intersegments 22/23–29/30. Very rarely, in addition to markings in 16/17 and 19/20, 4 pairs of circular markings in XVIII, 2 pairs being presetal and 2 pairs postsetal, the anterior pair and posterior pair lying median to *a* lines, the two other pairs in *ab*; or a presetal and a postsetal pair of circular markings in XVIII in addition to the markings in 16/17 and 19/20. Tumescence in the vicinity of ventral setal couples of the spermathecal region occurs constantly in VII,

usually in VIII, and commonly in IX. Female pores in *a* lines, midway between the setal arc and the anterior margin of XIV. Spermathecal pores in *ab* or in *a* line or slightly median of *a* on minute papillae almost concealed in the intersegment; the posterior pair 1.2 mm, 0.13 body circumference apart.

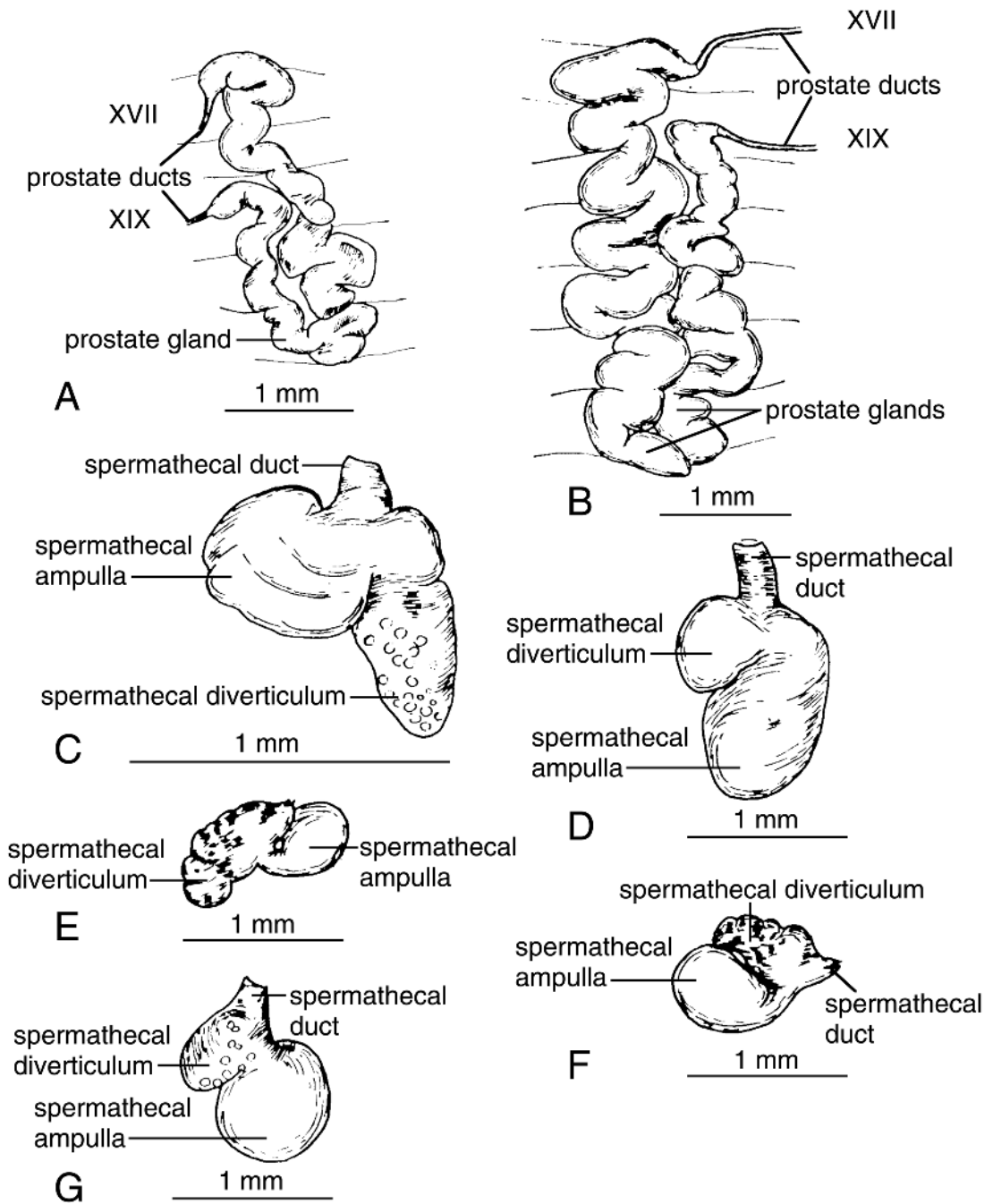
Thickest septa 6/7–8/9, moderately strongly thickened. Supra-oesophageal vessel traceable in VII–½XIV, a discrete strongly developed vessel. Last hearts in XIII; latero-oesophageal in X–XIII; dorsoventral commissurals in VI–IX also valvular. Gizzard moderately large, highly compressible, in V; oesophagus lacking pouching. Intestinal origin ½XVI or XVII; a low dorsal typhlosole



**Figs 122, 123.** *Diploptrema shandi* Jamieson and Dyne, 1976. **122**, genital field of Paratype 29; **123**, genital field of Paratype 39. [After Jamieson and Dyne 1976]

commencing, though still rudimentary, in XXI. Nephridia simple throughout, with thin-walled ducts entering the body wall in *d* lines; long-necked moderately large preseptal funnels demonstrated in the anterior intestinal region. Medium-sized, iridescent sperm funnels free in X and XI; 2 pairs of large seminal vesicles with large, conspicuous loculi in IX and XII, the posterior slightly the larger. Prostates, long coiled tubes, the moderately slender muscular ducts

travelling transversely within the segment of origin and entering intracoelomic parietal glands; both pairs of prostates extending to XXIV or XXV; the anterior pair therefore conspicuously the longer. Penial setae short, strongly curved, with an approximately semicircular bend; tip often recurved; ornamentation confined to ectal eighth but not pronounced, comprising a few scattered groups of bract-like teeth; length of mature seta 1.37 mm; midshaft diameter 30  $\mu$ m. Length of



**Fig. 124.** *Diploptrema shandi* Jamieson and Dyne, 1976: **A**, prostates of Paratype 28; **B**, prostates of Holotype; **C**, left spermatheca of IX, Paratype 29; **D**, right spermatheca of IX, Holotype; **E**, right spermatheca of VIII, Paratype 28; **F**, right spermatheca of IX, Paratype 28; **G**, right spermatheca of IX, Paratype 1.

[After Jamieson and Dyne 1976]

mature genital seta 0.95 mm; midshaft diameter 21  $\mu$ m. Ovaries fan-shaped with large oocytes; large ovisacs in XIV. Posterior pair of spermathecae slightly the larger; ampulla large, sacciform, diverticulum shorter and bulbous continuous with the short duct in such a way that the ampulla appears a sessile appendage of the diverticulum; the thick walls of the diverticulum with numerous large intramural sperm chambers; length of right spermatheca of IX 1.6 mm; ratio of total length: length duct = 5.8; ratio length: length diverticulum = 2.5.

### Remarks

The combination of a midventral pad in 16/17, anteriorly bounding the male genital field, seminal vesicles in IX and XII, and the bulbous (not digitiform tubular or tongue-shaped) diverticulum diagnoses *D. shandi*.

### *Diploptrema socialis* Dyne, 1987

(Figs 125, 126D-F)

*Diploptrema socialis* Dyne, 1987: 4–6, figs 3, 7–9.

**TYPE LOCALITY:** NT, 13°05'S 131°14'E, Upper Adelaide River Experimental Station, Adelaide River Floodplain, solodic soil. Coll. B. Wood, 8 March, 1984.

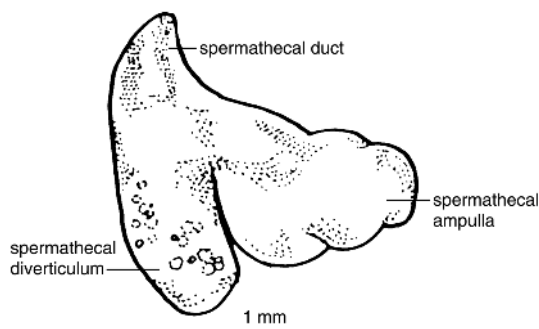
**HOLOTYPE:** NTM Wo6

**PARATYPE:** NTM Wo7 (1 semimature specimen)

### Description (after Dyne 1987)

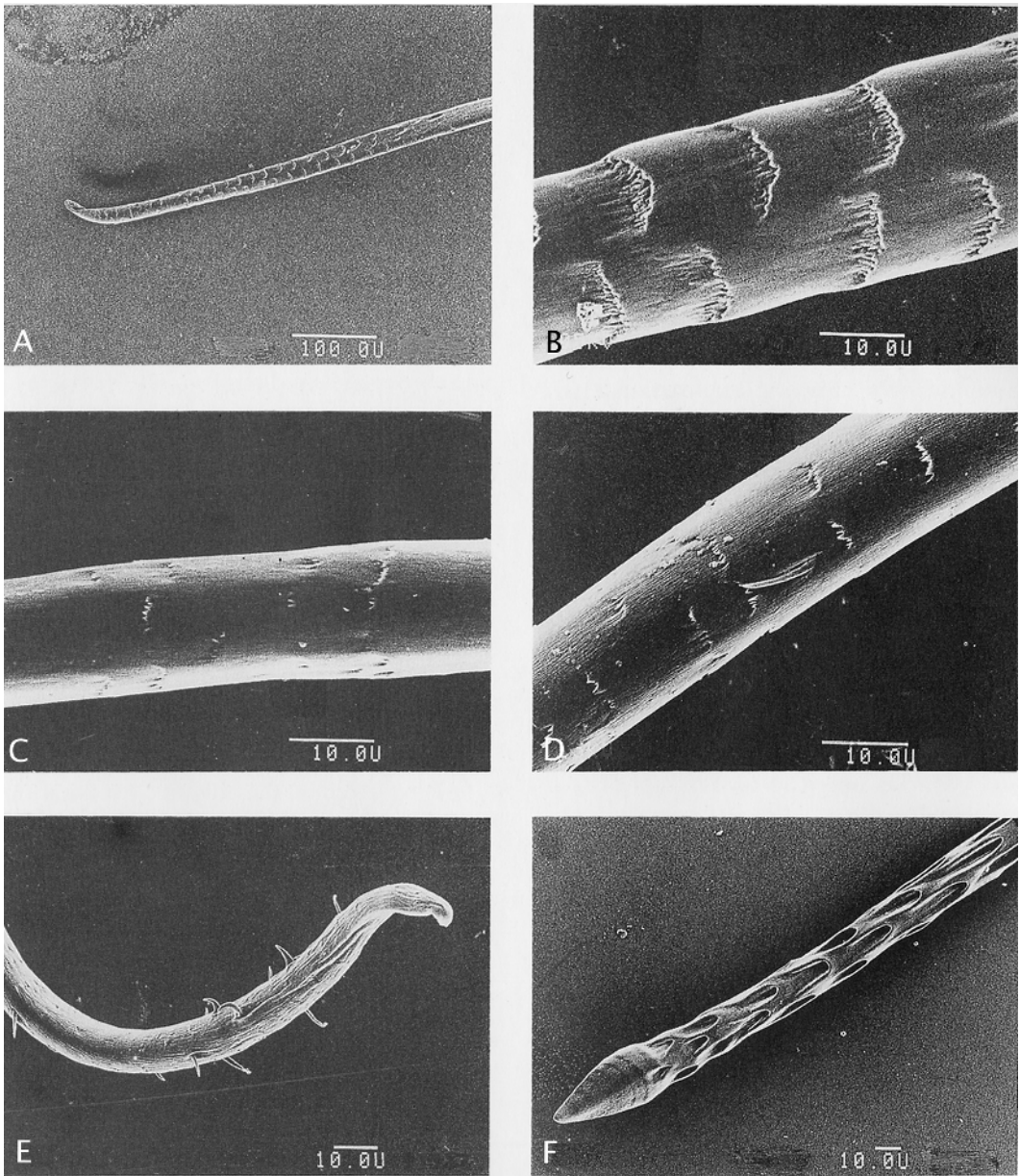
Length 47–52 mm. Width 1.5 mm. Segments 103–105. Prostomium epilobous 1/2 closed. Body uniform in diameter throughout, but segments of the caudal extremity much reduced in size and compressed longitudinally. First dorsal pore not demonstrable with certainty (?absent). Setae closely paired throughout, ventral setal couples present in XVIII, modified as penial setae in XVII and XIX, and as genital setae in VIII; in XII,  $aa:ab:bc:cd:dd = 10.1:3.3:13.9:3.6:48.6$ . Clitellum not developed. Male field a simple, rectangular depression extending from mid XVII to 19/20; porophores situated at the edges of this concavity, atop small, but definite papillae. The porophores of a side joined by ill-defined seminal grooves that traverse the raised lateral rims of the male field. Male pores not demonstrable. No accessory markings present. Female pores a minute pair of presetal slits in XIV; spermathecal pores indistinct, in 7/8 and 8/9, aligned with the ventral setal pairs.

Only septal partitions 8/9–10/11 show any degree of muscularisation; 6/7 and 7/8 somewhat thickened, as is 11/12, the remainder thin. Dorsal blood vessel single throughout. Last hearts in XIII.



**Fig. 125.** *Diploptrema socialis* Dyne, 1987, right spermatheca of IX, Holotype. [After Dyne 1987]

A supra-oesophageal vessel present from mid-VIII to XIII; the major commissurals (i.e. those in X–XIII) appear to be exclusively connected to the supra-oesophageal vessel, having no communion with the dorsal vessel. Anteriad commissurals certainly dorsoventral, but their continued association with the supra-oesophageal not certain. Gizzard, in V, moderately large and shiny, with obvious proventriculus; oesophagus moniliform, vascular, in VI–XV. Intestine commences abruptly in XVI, broadening to maximal width by the succeeding segment; typhlosole lacking. Ingesta: fine soil particles, silica grains and some blackened organic remains. Holonephric; anterior tufted nephridia absent. In the intestinal segments, the coils of each nephridial body enveloped in ?connective tissue, giving the units a wafer-like appearance. Nephridial ducts uniformly enter the parietes in *d* lines. Holandric; 2 pairs of small, weakly iridescent spermathecal funnels present in X and XI, with finely loculate seminal vesicles seen in IX and XII. Vasa deferentia not traceable. Prostate glands tubular: long, sinuous and delicate, anterior pairs extending posteriad through septal walls into segments XXI or XXII; posterior pairs somewhat shorter, extending to XXII. Prostatic ducts narrow, hardly muscular. Both pairs of organs associated with penial seta follicles that penetrate into succeeding segments, the latter are joined to the prostates by diaphanous connective tissue, and to the body wall by limited copulatory musculature. The reddish setae ornamented over distal half with a variable number of fairly long, acuminate spines projecting at an acute angle to the setal shaft; these are interspersed with short circumferential bracts of irregularly jagged teeth. Latter ornamentation may predominate in some setae, but some spines always present. Ovaries not seen, but small, plicate oviducal funnels present in XIII. Spermathecae 2 pairs in VIII and IX, subequal, consisting of a lobulated, sacciform



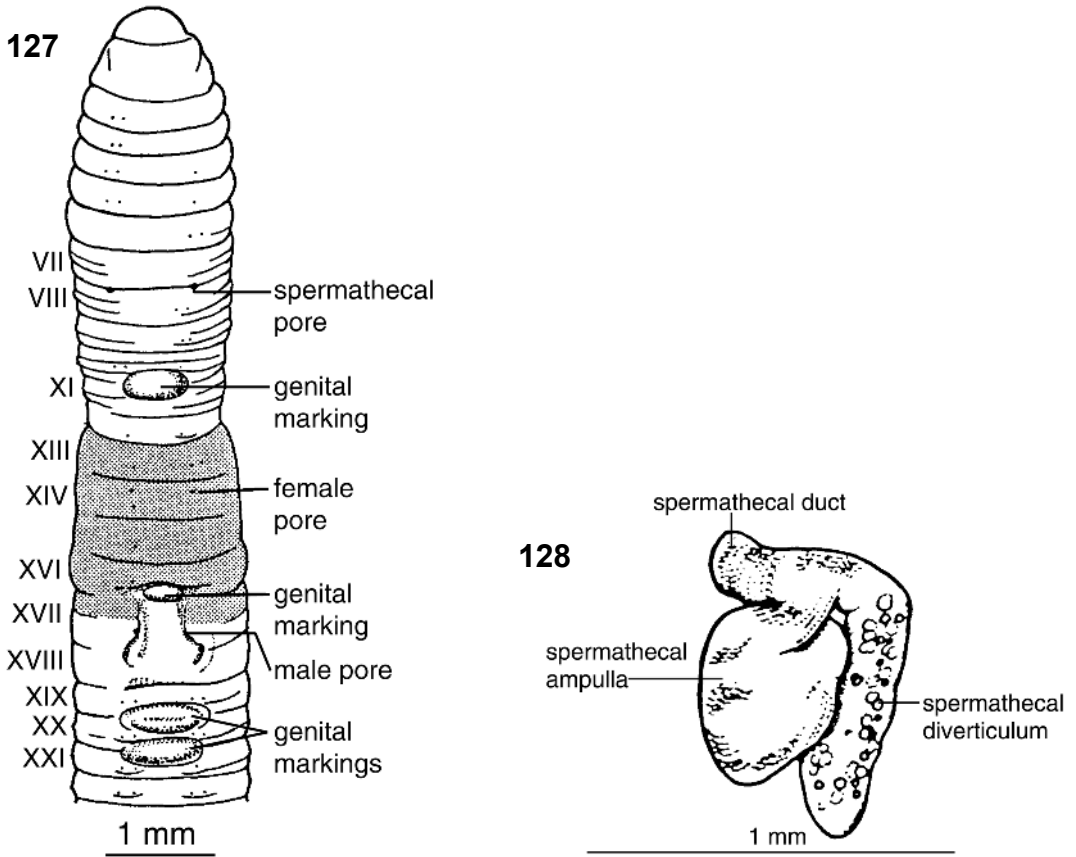
**Fig. 126**, penial and genital setae of *Diplotrema*: **A-C**, *D. planumfluvialis*, penial; **D,E**, *D. socialis*, penial; **F**, *D. socialis*, genital seta. [After Dyne 1987]

ampulla joining diverticulum/duct axis at 45°, and a short, blunt diverticulum iridescent with inseminate leading directly to a short duct. Length right spermatheca of VIII 0.9 mm. Genital seta follicles present in VIII only. Setae sculptured by regularly and closely disposed deep, axially directed excavations. Apical portion of seta swollen, terminating in a rounded point.

#### Remarks

The spinose penial setae of *D. socialis* are reminiscent of those seen in *D. mantoni* as is the construction of the spermathecae. In other respects

(genital markings, typhlosole, position of seminal vesicles, length of prostates, position of nephropores) the two species exhibit little affinity. It is noteworthy, however, that the Manton River (from which the latter species was collected) joins the Adelaide River only some 40 km northwards (downstream) from the type-locality of the two new species. *D. socialis* is referable to the *D. shandi* species-group (Dyne 1987).



**Figs 127, 128, *Diplotrema gracilis* sp. nov., Holotype. 127, genital field; 128, left spermatheca of VII.**



MICROSCOLECIN NORTHERN TERRITORY *DIPLOOTREMA* SPECIES*Diplootrema gracilis* sp. nov.

(Fig. 127, 128)

**TYPE LOCALITY:** NT, 12°34'S 131°16'E, Fogg Dam Road, near Darwin, in loamy soil. Coll. W. Nash, 12 Dec. 1974.

**HOLOTYPE:** QM 2931.

**Description**

Length 21.5 mm. Width (midclitellar) 1.6 mm. Segments 85. Form circular in cross-section, pigmentless buff in alcohol. Prostomium epilobous 1/2, open, the lateral margins of the dorsal tongue strongly convergent posteriad. First dorsal pore 7/8. Setae 8 per segment in regular longitudinal rows, commencing on II, the ventral setal couples of XVII modified as penial setae. Nephropores seen very slightly below *c* lines, anteriorly in their segments. Clitellum annular, XIII–2/3 XVII. A single pair prostatic pores on XVII in *ab*, on the median aspects of a pair of very prominent longitudinal ridges with a deep depression between them, and which continue, though decreasing in height, to the equators of XVI and XVIII. The male pores are possibly united with the prostatic pores, though this is not demonstrable internally. Accessory markings a midventral, transversely oval pad in each of intersegments 10/11, 16/17, 19/20 and 20/21; each with a peripheral rim and more translucent central area; that in 16/17 small, extending from the equator of XVI only a short distance into XVII, and laterally into *ab*; the other 3 markings extending to, though not including, the setal arcs of the segment preceding the intersegment, and laterally well into *ab*, or as far as *b* lines. Female pores small, but distinctly visible in mid *ab*, midway between the setal arc and the anterior border of XIV. Spermathecal pores 1 pair in 7/8, on small, oval papillae in *b* lines.

All septa diaphanous, with no conspicuous preclitellar thickening. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal blood vessel well developed, visible in VIII–XIV. Last hearts in XII; those in X–XII latero-oesophageal, each with a thick connective to the supra-oesophageal, but connectives to the dorsal vessel not demonstrated with certainty. Gizzard very large, muscular, though compressible, in V, but deflecting succeeding septa into X. Oesophagus expanded and with circumferential vascular striae in XII–XIV, especially XIII, but calciferous glands absent. Intestinal origin in XVII, muscular thickening absent, but a low

dorsal ridge present which may be considered a rudimentary typhlosole. Nephridia simple, stomate, avesculate exonephric holonephridia throughout commencing in II; their slender ducts discharging presetally in *c* lines. Relatively very large, strongly iridescent sperm funnels in X and XI. Racemose seminal vesicles a pair in each of IX and XII; testis sacs absent. Prostates discharging in XVII but first running from XXII to XVI; of the slender type but strongly flattened and deeply incised at the septa; ectal muscular duct passing posteriorly from XVI into XVII and then bending medianwards to reach the pore. Vas deferens traced to the median extremity of the prostate duct but possibly running further posteriorly (?). Penial setae fairly short, very fine and delicate, the follicles with little copulatory musculature. Ovaries consisting of several strings of large oocytes, and funnels in XIII; ovisacs absent. Spermathecae 1 pair, in VIII, discharging anteriorly; each with an ovoid ampulla, and entally wide duct which is joined laterally by an inseminated clavate diverticulum with a small number of slight protuberances corresponding with internal seminal chambers; length of right spermatheca of VIII 1.14 mm (base of diverticulum to pore). Ratio total length: length duct = 2.4.

**Remarks**

This species was tentatively placed in *Rhododrilus* by Dyne (1984, unpublished). Location of the last hearts in XII is most unusual in Australian members of the Acanthodrilinae (though apparently widespread in New Zealand). The only other known example was recorded by Jamieson and Dyne (1976) for *Diplootrema minuta*, also from the Northern Territory. In the latter paper, it was conceded that location of the last hearts in XII in *D. minuta* might represent a secondary regression associated with very small body size, rather than necessarily pointing to a primitive status for the species. The re-occurrence of this condition in *D. gracilis*, a species very similar in size to *D. minuta*, lends support to that concept. An arid barrier now intervenes between *D. gracilis* and easterly species of *Diplootrema*, including other microscolecin species. The Gulf of Carpentaria region remains largely unsampled, but the prevailing climatic conditions would preclude all but a scattered, relictual oligochaete fauna.

Location of the spermathecal pores in 7/8 sets *D. gracilis* apart from the three microscolecin Queensland species, in which they lie in 8/9.

*Kayarmacia* Jamieson, 1997

*Kayarmacia* Jamieson, 1997: 253–255.

**TYPE SPECIES:** *Kayarmacia adelphicus* Jamieson, 1997

**Diagnosis**

A pair of combined male and prostatic pores, associated with penial setae, on XVII. Spermathecal pores 1 pair, in intersegmental furrow 7/8. Gizzard in V. Oesophagus lacking calciferous glands. Holonephric; nephridia avesculate. Holandric. Prostate a single pair of tortuous tubes, each with an exceptionally long tortuous muscular duct which opens in common with the thick and muscular ectal end of the vas deferens (ejaculatory duct). Spermathecae a pair in VIII; diverticulum, with nacreous sperm masses.

**Description (emended from Jamieson 1997)**

Small worms, less than 75 mm long. Dorsal pores (always?) present. Setae 8 per segment, closely paired; the lateral couple (*cd*) narrower than the ventral couple (*ab*). Clitellum anterior to the male pores; annular. A pair of combined male and prostatic pores, associated with penial setae, on XVII. Genital markings present in the vicinity of the male pores. Genital tumescence and modified ventral setae present or absent in the spermathecal region. Female pore(s) presetal in XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8.

Dorsal blood vessel single. Last hearts in XIII, those in X–XIII large, heart-like and latero-oesophageal, the connective to the supra-oesophageal vessel larger than that to the dorsal vessel; commissurals in IX anteriorly slender, with dorsal connective only. Gizzard large, strongly muscular in V. Oesophagus lacking calciferous glands. Intestine commencing in XVII. Holonephric; avesculate ducts apparently discharging in mid *bc* or *c* lines; true anterior tufting not developed. Holandric. Racemose seminal vesicles in IX and XII. Ovaries in XIII. Prostate glands extending through several segments; a single pair of tortuous tubes, each with an exceptionally long tortuous muscular duct which winds forwards to open at the male pore in common with the thick and muscular ectal end of the vas deferens (ejaculatory duct). Spermathecae a pair in VIII, opening at the anterior border; diverticulum, with nacreous sperm masses.

**LIST OF SPECIES OF *KAYARMACIA***

1. *Kayarmacia adelphicus* Jamieson, 1997
2. *Kayarmacia bursatus* sp. nov.
3. *Kayarmacia cochlearis* sp. nov.
4. *Kayarmacia queenslandicus* (Michaelsen, 1916) (*Rhododrilus*)

**Distribution:** Queensland: Cape York Peninsula to 20°S.

**Remarks**

*K. adelphicus* was chosen as the type species for *Kayarmacia* as synonymy of *K. queenslandicus* with Michaelsen's species, though made with confidence, was subjective. Later changes to its synonymy, though unlikely, would cause confusion if *K. queenslandicus* were selected as the type species.

Michaelsen (1916) placed the Alice River specimens in *Rhododrilus*, features of this genus being of location of male pores in segment XVII, presence of a gizzard, and absence of nephridial bladders. However, these are insufficient reasons (Jamieson 1997) for considering *R. queenslandicus* to be congeneric with the New Zealand type species of the genus, *Rhododrilus minutus* Beddard, 1889, as the latter species has four pairs of spermathecal pores and, more significantly, has the male and prostatic pores located separately on XVII. The mere presence of male and prostatic pores on XVII whether combined or separate is not unique to one genus, as it is seen *inter alia* in the acanthodriline genus *Microscolex* and is the typical condition in the Ocnodrilinae and Eudrilidae. Nevertheless, it is clear that location on XVII represents a microscolecin reduction from an acanthodrilin arrangement of male pores (male pores on XVIII, prostatic pores on XVII and XIX) and that *Kayarmacia* is referable to the subfamily Acanthodrilinae and not to the Megascolecinae. Origin from a stock which would have been identifiable as *Diplotrema* is likely as the type-species of *Kayarmacia* has scalloped genital setae of the *Diplotrema* type. Two new species, *K. bursatus* and *K. cochlearis*, are added here.

The thickening of the distal ends of the vasa deferentia and their opening in common with the unusually long prostate ducts distinguishes *Kayarmacia* from other megascolecid genera (ducts are confluent in *Microscolex dubius* and, less intimately, in *M. phosphoreus* but there are not thickened). Inclusion in the Ocnodrilidae, a family in which male and prostate ducts may be

swollen is precluded by several features, including the non-ocnerodriline condition of the oesophagus. Native Ocnerodrilidae are unknown from Australia.

*Rhododrilus glandifera* Jamieson, 1995, is excluded from *Kayarmacia* by location of the spermathecal pores in intersegmental furrow 8/9, not 7/8, and, more significantly, the absence of thickening of the vasa deferentia, and the minute size of the apparently separate prostate ducts. That *R. glandifera* is congeneric with *Rhododrilus* is no longer sustainable. It is here transferred to

*Diplotrema*, as a microscolecin species, as supported by molecular analysis (Fig. 3). The position of *Kayarmacia* relative to *Diplotrema* requires investigation through molecular analysis.

Presence of scalloped genital setae of the *Diplotrema* type in *K. adelphicus* suggests origin of the *Kayarmacia* from a common stock with *Diplotrema*. Location of spermathecal pores in 7/8, rather than 8/9 as in the microscolecin Queensland species of *Diplotrema*, suggests independent origin of the microscolecin condition relative to these.

## KEY TO AUSTRALIAN SPECIES OF *KAYARMACIA*

- 1 a. Genital setae (of the gouged *Diplotrema* type) present in the spermathecal region. Female pore paired ..... ***K. adelphicus***  
 b. Genital setae absent. Female pore paired or single. .... 2
- 2(1b) a. Female pore single, midventral ..... ***K. bursatus***  
 b. Female pores paired. .... 3
- 3(2b) a. Genital markings include a very large, tumid pad extending antieriad from 19/20 to the bases of the prostatic porophores, produced into a cuneiform projection to mid-d-XVII. Female pores in *ab* (closer to *a* lines). . ***K. cochlearis***  
 b. Genital markings include indistinct hemispheroidal midventral marking present presetally in XVIII; a larger indefinite tumescence presetally in XIX, or a hemispheroidal midventral genital marking present post-setally in XVIII. Female pores anteromedian of seta *a* of XIV ..... ***K. queenslandicus***

### ***Kayarmacia adelphicus* Jamieson, 1997**

(Figs 129–132)

***Kayarmacia adelphicus*** Jamieson, 1997: 255–257, fig. 24–27, 39.

**TYPE LOCALITY:** (1) QLD, 14°15'30"S 144°27'30"E, Cape Melville National Park, along creek bank, closed canopy, altitude ca 100 m, in humic sandy soil under closed canopy on a creek bank near the edge of the Cape Melville Altanmoui granite boulder fields. K.R. McDonald, L.A. Jackson, 24 Feb 1995.

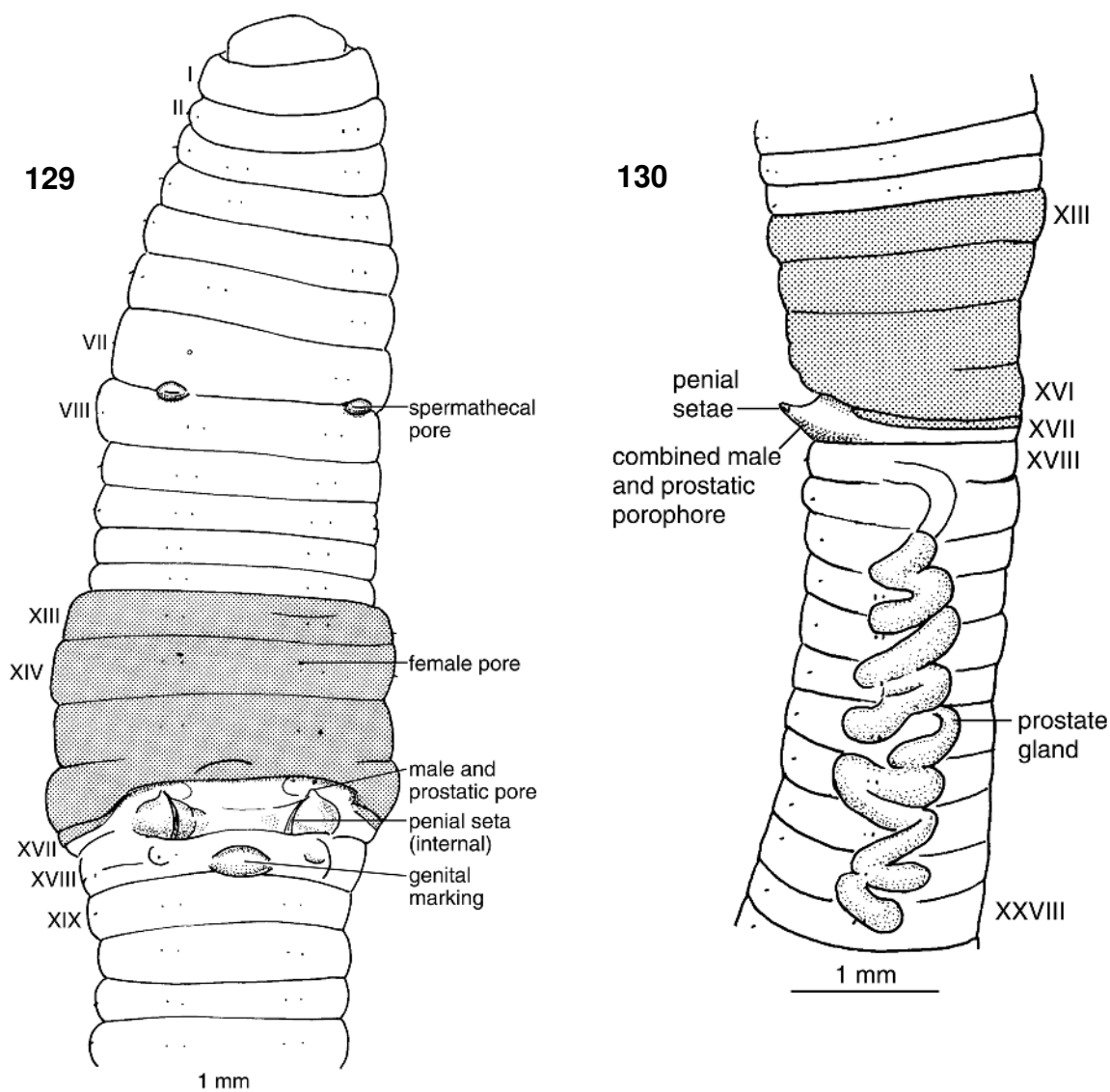
**PARATYPE LOCALITIES:** (1) As above. (2) Same, 14°16.9'S 144°27.5'E, 18 Feb 1995.

**HOLOTYPE:** (1) QM G213378 ex211497 (part) (includes microscope slide of male ducts).

**PARATYPES:** (1) P1–5 QM G211497 (with several not designated types). (2) P6 and 7 QM G211495.

### **Description (after Jamieson 1997)**

Length 25–39 mm. Width (midclitellar) 1.8–2.6 mm. Segments 102. Pigmentless greyish buff in ethanol. Prostomium pro-epilobous or epilobous 1/2. Peristomium approximately as long as segment II. Dorsal pores sporadically visible from shortly anterior to the clitellum (verified by exudation of alcohol when specimen is placed in water). Setae closely paired; in XII, *aa: ab: bc: cd: dd* = 8.2: 1.0: 7.7: 0.9: 18.1; or 18.1: 2.2: 16.9: 1.9: 40.0%. Clitellum in XIII to anterior XVII; annular but ventrally interrupted from the anterior third of XVI posteriorly, to about mid *bc* by the male field; setae and intersegmental furrows present on it. A pair of large, globose but anteriorly pointed strongly protuberant papillae each bearing the combined male and prostatic pore on XVII; in *ab*; the walls of the papillae diaphanous and revealing internally the large penial setae which support its anterior protrusion, or the penial setae strongly protuberant. Genital markings a pair of indistinct swellings, at setae *ab* of XVI and XVIII; a midventral elliptical papilla postsetally in XVIII

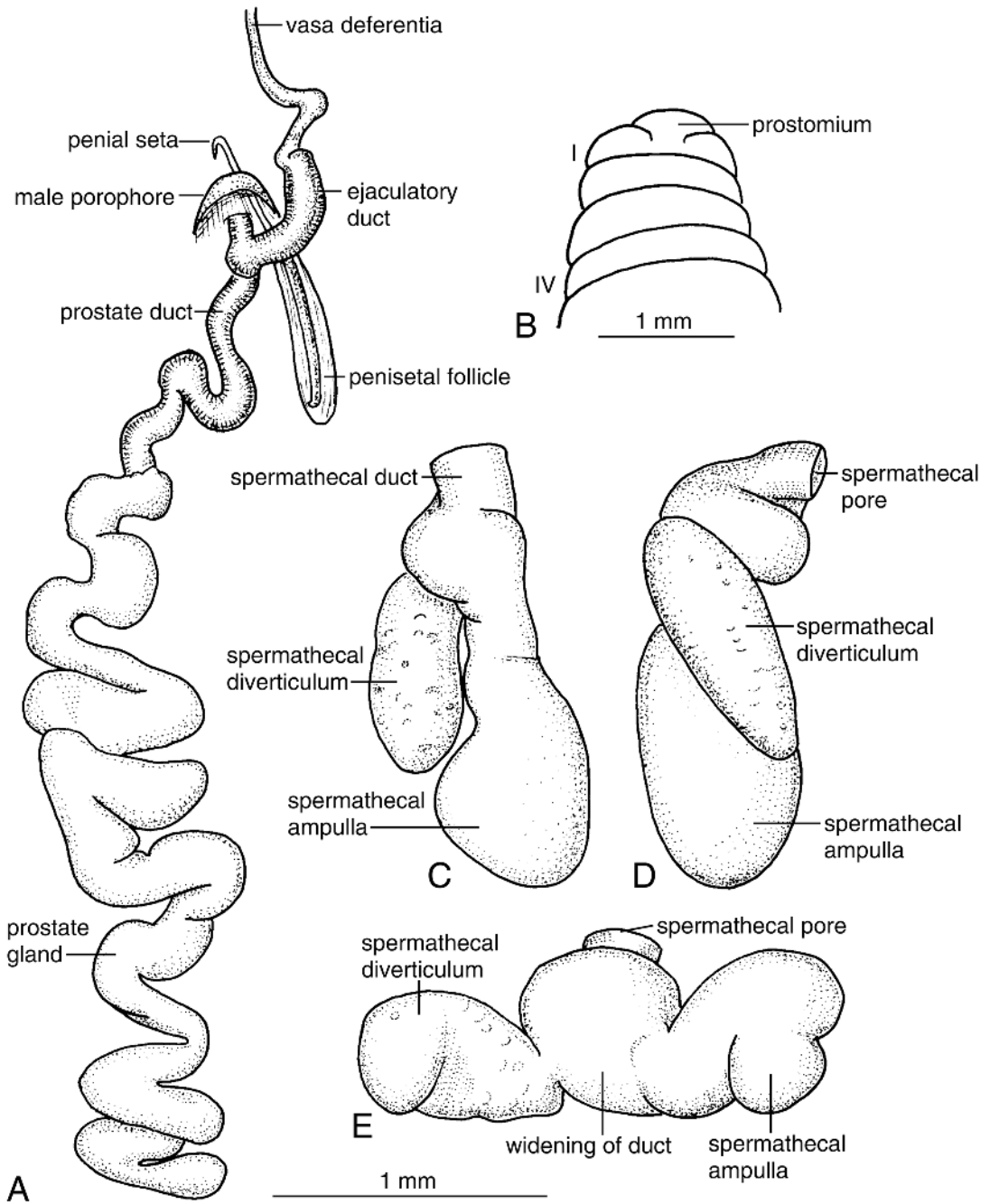


**Figs 129, 130.** *Kayarmacia adelphicus* Jamieson, 1997, Holotype. **129**, genital field; **130**, left lateral view of male genital region of holotype, showing prostate gland seen through the body wall—the connection of the prostate with the male pores is not visible. [From Jamieson 1997]

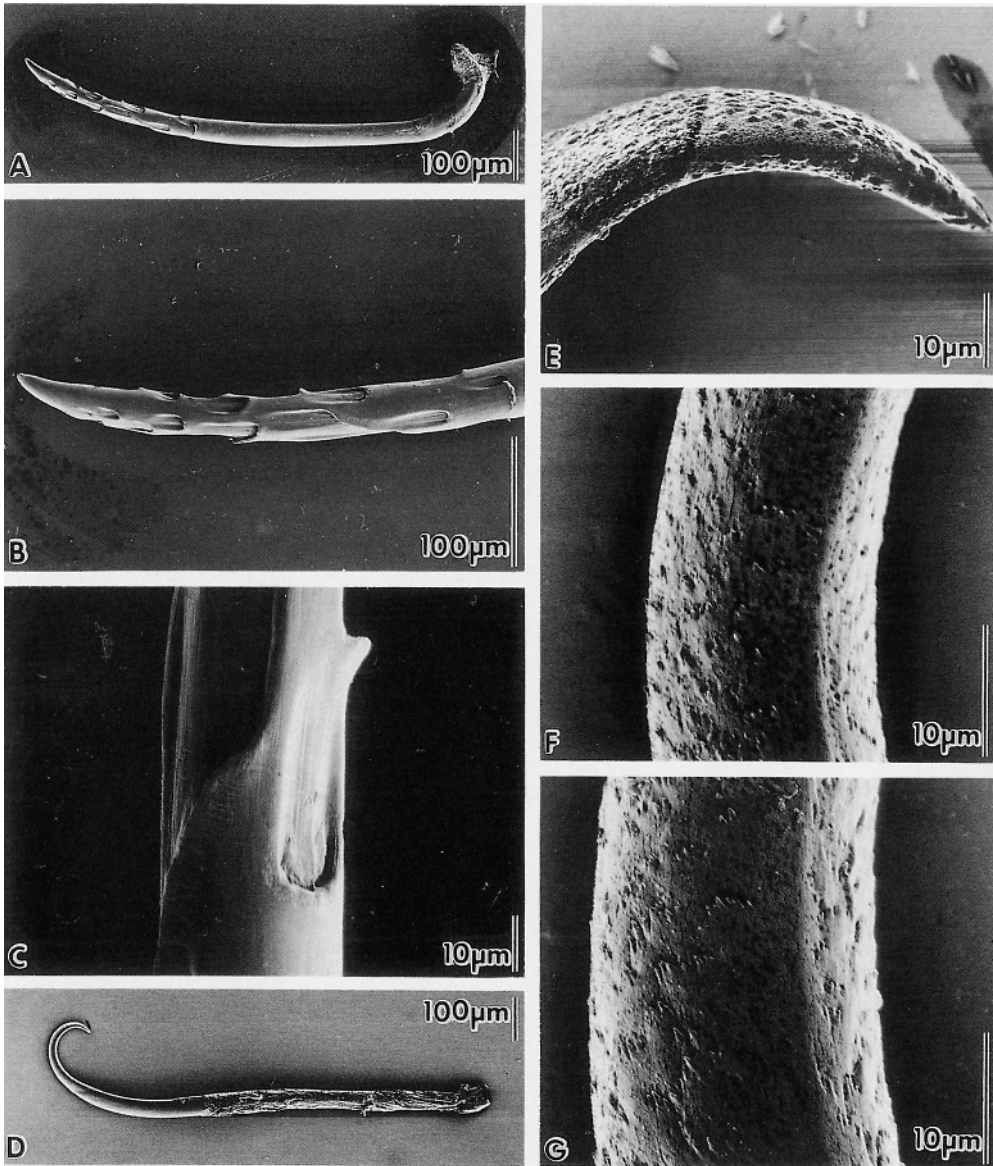
or in XVI. Genital tumescence and modified ventral setae developed on the right side in VII or paired in IX. Female pores minute, immediately anterior to setae *a* of XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8, shortly lateral of *b*; each a lateral slit in an oval papilla.

Septa 8/9 and 9/10 the thickest, moderately strongly thickened. Dorsal blood vessel single. Last hearts in XIII, those in X–XIII large, heart-like and latero-oesophageal, the connective to the

supra-oesophageal vessel larger than that to the dorsal vessel; commissurals in IX anteriorly slender, with dorsal connective only. Gizzard very large, strongly muscular but compressible, ellipsoidal though widening anteriorly, in V. Oesophagus lacking calciferous glands. Intestine commencing, with abrupt expansion, in XVII. Holonephric; nephridial bodies commencing in II; avesiculate ducts apparently discharging in mid *bc*; anterior tufting not developed. Holandric;



**Fig. 131.** *Kayarmacia adelphicus* Jamieson, 1997: **A**, left prostate and male duct, with penisetal follicle of Holotype; **B**, dorsal view in region of prostomium of Holotype; **C**, **D**, two views of left spermatheca of Holotype; **E**, left spermatheca of Paratype 2. [From Jamieson 1997]



**Fig. 132.** *Kayarmacia adelphicus* Jamieson, 1997: **A-C**, left genital seta of VII I of Paratype; **D-G**, right penial setal of Holotype. [After Jamieson 1997]

iridescent sperm funnels in X and XI. Large, several lobed racemose seminal vesicles in IX and XII. Small ovaries, with few oocytes, in XIII. Prostate glands visible externally through the body wall in the holotype extending from XVII to XXVIII; a single pair of tortuous tubes, each with an exceptionally long tortuous muscular duct which winds forwards to open at the male pore in common with the equally thick and muscular ectal end of the vas deferens (ejaculatory duct); the prostate duct and ejaculatory duct pass separately but in contact to the tip of the male porophore (confirmed in cleared mount). Penial setae, only 1 on each side; stout, ectally curved to form a hook; length 1.2 mm, greatest, basal, width ca 70 µm; ornamentation consists of droplet-like or many wart-like elliptical prominences on the 'dorsal' and 'ventral' surfaces of the curvature, the sides of the latter being smooth; on the ventral surface, however, the prominences are reduced to minute scattered but densely situated points or cicatrices. Genital setae present on right in VII or bilateral in VIII; length of left genital seta of VIII, 0.76 mm; shaft gently curved but a short basal region strongly curved; tip pointed, very slightly expanded beneath the point; ornamentation four (?) longitudinal series, each of about five large gouges or notches. Spermathecae a pair in VIII, opening at the anterior border; each with a large ovoid ampulla; the duct of which consists of three regions in longitudinal succession: an ental third which is approximately tubular and is well demarcated from the ampulla, a swollen intermediate region (sometimes as wide as the ampulla) which receives the diverticulum, and an ectal third which forms a wide, short, muscular, tubular duct. Diverticulum elongate ellipsoid, filled with nacreous sperm masses but uniloculate, with a narrow connection to the spermathecal duct. Length left spermatheca = 1.7 mm; length ampulla = 0.88 mm; ratio length spermatheca: length duct = 2.1; length diverticulum = 1.0 mm.

### Remarks

*Kayarmacia adelphicus* is morphologically very close to the prior *K. queenslandicus* (q.v.) but geographical separation by the Great Dividing Range suggests that the presence of genital setae, apparently always absent from *K. queenslandicus*, indicates vicariation of the two taxa from a common ancestor. Strong support for recognising the two as separate species is seen in the very different ornamentation of the penial setae. It consists of scattered droplet-like prominences in *K. adelphicus* contrasting with tooth rows, which 'ventrally' are united in extensive transverse rows in *K. queenslandicus*.

The distinctive structure of the male and prostatic ducts seen in both species was regarded as meriting generic status. The genital setae of *K. adelphicus*, with longitudinal series of large gouges or notches, are of the type seen also in *Diplotrema* and the New Caledonian genus *Acanthodrilus* and indicate relationship with these genera (Jamieson 1997).

### *Kayarmacia bursatus* sp. nov.

(Figs 133, 134)

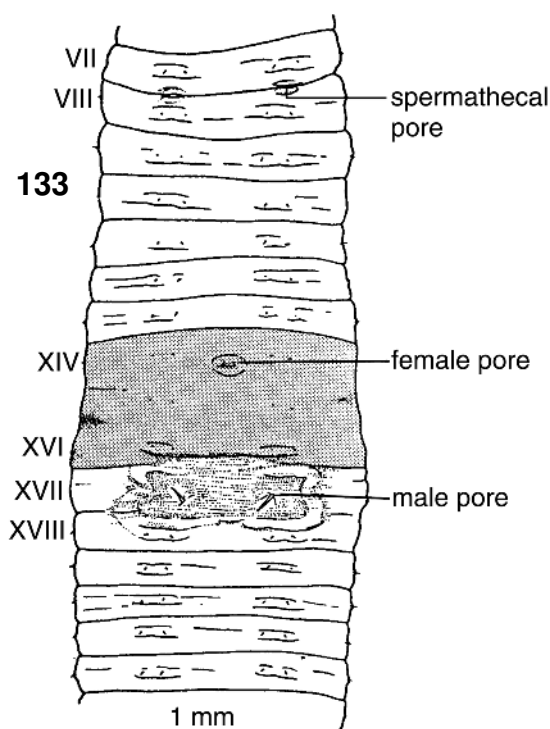
**TYPE LOCALITY:** Qld, 18°01'S 144° 15'E, Elizabeth Creek, 47 km north of Mt Surprise, in the gravel bed of a flowing stream. Coll. M. Shand and W. Nash, 13 Nov. 1974.

**HOLOTYPE:** QM G 8874.

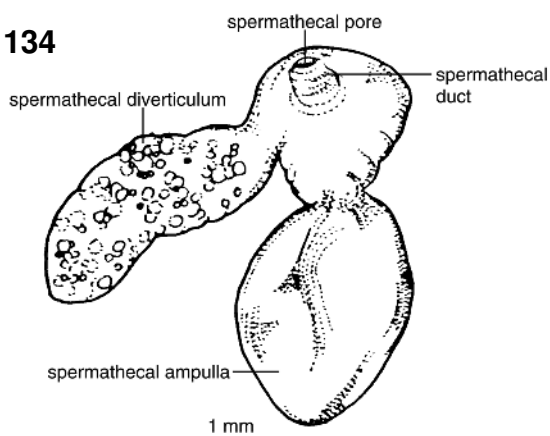
### Description

Length 34 mm. Width (midclitellar) 2.4 mm. Segments 97. Uniformly circular in cross-section throughout, greyish in alcohol. Prostomium propilobous; first dorsal pore 9/10. Setae 8 per segment, commencing in II; ventral setal couples of XVII modified as enlarged penial setae. Nephropores not visible externally. Clitellum annular, well developed in XIV–XVI, dorsal pores and setae only partially obscured. Combined male and prostatic pores associated with penial setae on low mounds in XVIII. The male field is a slightly depressed area bounded anteriorly by the clitellum and extending posteriorly to the extreme anterior portion of XVIII; the field is delimited laterally by jagged glandular strips. Accessory markings absent. Female pore unpaired, median, in line with the setal arc, in XIV, within an oval depression. Spermathecal pores a single pair of slits in 7/8, within slightly protuberant lips, in *ab*.

No septa strongly thickened, but septa 6/7–10/11 slightly thickened with muscular bands; septum 5/6 thin. Dorsal blood vessel single; supra-oesophageal vessel present VII–XIII, well developed anterior of X, adherent to the roof of the oesophagus; last hearts in XIII, those in XII and XIII with definite connections to both dorsal and oesophageal vessels; remaining hearts appear to receive connectives solely from the supra-oesophageal vessel. Gizzard small-medium, soft and compressible, though conspicuously muscular, in V; oesophagus VI–XV, moderately vascular, pouching or calciferous glands absent; intestinal origin XVI; a very low dorsal typhlosole, associated with an insinking of the dorsal vessel, commences in XXII. Holonephric throughout, with medium-sized preseptal nephrostomes and thin-walled avesculate ducts entering the parietes in *d* lines; anterior tufting absent. Holandric; 2 pairs iridescent sperm funnels in X and XI; 2 pairs large



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**Figs 133, 134.** *Kayarmacia bursatus* sp. nov., Holotype. 133, genital field; 134, right spermatheca.

racemose seminal vesicles in IX and XII, the former pair the more extensive; vasa deferentia conspicuous as closely paired, slightly iridescent tubes closely adherent to the body wall on each side, slightly lateral of *b* lines; the vasa deferentia tightly coiled for the first 2 segments from their respective origins, becoming straight, each pair uniting in XVI to form a conspicuously dilated,

thick-walled duct in XVII that fuses with the prostatic duct within the parietes. Prostate glands a single pair of tightly coiled tubular organs extending posteriorly to XXII, with straight, thick-walled ducts entering the body wall in XVII. Penis setal follicles prominent, extending to XVIII, attached to the body wall just below the dorsal line by a single muscular band passing across the glandular portion of the prostate. The setae curving fairly strongly, the ectal region ornamented with irregularly disposed lines of fine to coarse teeth, arranged in bracts, or as discrete individuals; these become more densely aggregated near the tip, which is simple. Ovaries, consisting of a single, large, palmate cluster of oocytes on each side of the oesophagus, and medium-sized pleated funnels seen in XIII; ovisacs absent. Oviducts seen to enter the body wall in 13/14. Spermathecae a single pair in VIII, consisting of an ampulla divided into 2 distinct portions, and a sausage-shaped inseminated diverticulum; the ental portion of the ampulla is ovoidal, and connected by a short isthmus to the bulbous section from which arises the short duct; the diverticulum joins this section through a narrowed duct. Length of right spermatheca of VIII 1.3 mm, ampullal and diverticular sections of approximately equal length.

### Remarks

This species was tentatively placed in *Rhododrilus* by Dyne (1984, unpublished). However, he noted the similarity to *R. queenslandicus*, a species placed subsequently in *Kayarmacia* (Jamieson 1997), on erection of that genus. Dyne rightly noted that the shape of the spermathecae in *K. bursatus* is reminiscent of that of *K. queenslandicus*; the former apparently associated with the Lynd River system, which, not coincidentally, drains eventually into the Gulf of Carpentaria via the Mitchell River of which the Alice River (type locality of *K. queenslandicus*) is also a tributary. He considered that the two species might need to be synonymised if new collections in the region yielded intermediate forms.

Apparent differences from *K. queenslandicus* noted here are: dorsal pores commencing in 9/10, while in *K. queenslandicus* they are absent (Michaelsen 1916) or sporadically visible (Jamieson 1997) from shortly anterior to the clitellum; intestinal origin in XVI, not XVII; presence of a typhlosole; penial setae with irregularly disposed lines of fine to coarse teeth, arranged in bracts, or as discrete individuals, not in transverse rows with the sides smooth. These differences require confirmation from further material.



***Kayarmacia cochlearis* sp. nov.**

(Figs 135, 136)

**TYPE LOCALITY:** Qld, 20° 08'S:146° 05'E, 20 km west of Charter's Towers, in wet, black, clayey soil. Coll. W. Nash and M. Shand, 5 Feb 1975, 8 semi-mature specimens.

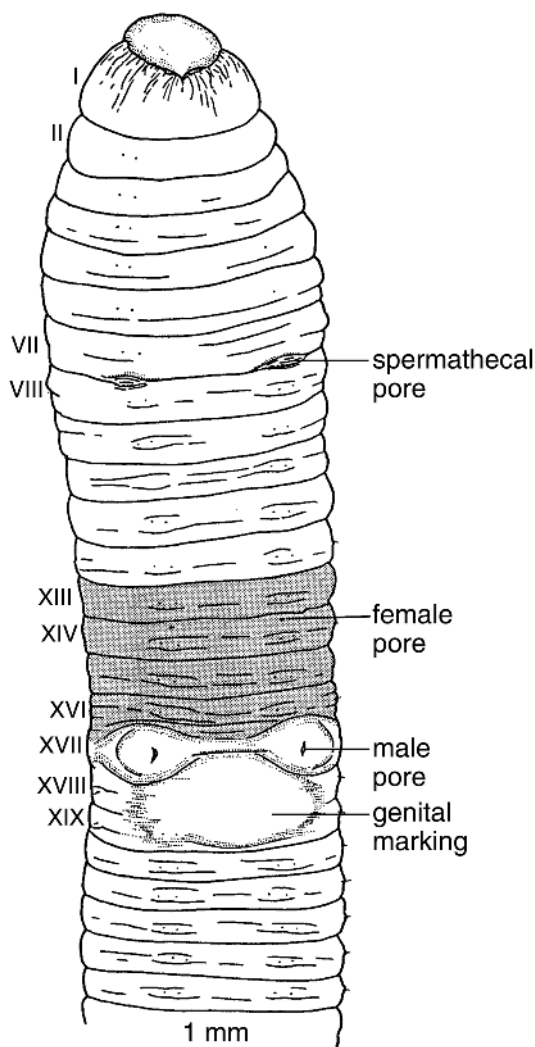
**HOLOTYPE:** QM GH2909. (Queensland Museum Catalogue states not received by Museum).

**PARATYPES:** QM GH2910. (Queensland Museum Catalogue states not received by Museum).

**Description**

Length 49, 49.5 mm. Width (midclitellar) = 2.6, 2.5–2.6 mm. Segments 127, 129 (H, P1). Pigmentless buff in alcohol, uniformly circular in cross-section throughout. Prostomium propilobous, peristomium with conspicuous furrowing. First dorsal pore 10/11 (imperforate). Setae 8 per segment, commencing on II. Setae *a* and *b* in XVII modified as enlarged penial setae. Nephropores inconspicuous externally. Clitellum undeveloped. Combined male and prostatic pores a single pair, on raised papillae in XVII; the latter fill the segment, and extend laterally almost to *c* lines. The porophores are coincident with the penial seta openings. Accessory markings a very large, tumid pad extends anteriorad from 19/20 to the bases of the porophore mounds, produced into a cuneiform projection between the mounds to mid-XVII, laterally, the marking extends to *b* lines (present in all examined specimens). Female pores in XIV, a pair of minute openings close to intersegment 13/14 in *ab* (closer to *a* lines). Spermathecal pores a single pair just lateral of *b* lines, in 7/8, with slightly tumid surrounds.

Septa 5/6, 6/7 moderately thickened, 7/8, 8/9, 9/10 strongly thickened with muscularisation, 10/11 moderately so, 11/12 slightly thickened. Dorsal blood vessel single, supra-oesophageal vessel present, strongly developed in VIII–XIV. Last hearts in XIII, commissurals only recognisable in X–XIII, all with definite connections to the supra-oesophageal vessel, but no apparent dorsal vessel connections. Gizzard medium sized, but not particularly thick-walled, compressible, in V. Oesophagus VI–XVI, pouching or calciferous glands absent; intestine commencing with conspicuous dilatation in XVII. Holonephric, with small preseptal funnels on delicate necks, and thin-walled ducts, entering the parietes in *d* lines; no tufting demonstrable in the pharyngeal region. Holandric, 2 pairs of small to medium iridescent sperm funnels and associated sperm masses free in X and XI; 2 pairs of finely racemose seminal vesicles in IX and XII, the former conspicuously the larger. Vasa deferentia conspicuous as close



**Fig. 135.** *Kayarmacia cochlearis* sp. nov., genital field of Holotype.

pairs of faintly iridescent coils on the body wall, particularly in XV–XVII; each pair is apparently fused after XV, where the single duct dilates considerably, forming a muscular, thickened tube, which joins the prostatic duct near its ectal end, just prior to its entering the body wall. Prostate glands a single pair of coiled tubular structures extending posteriorly into XXV. Prostatic ducts closely associated with penial seta follicles, which are connected to the body wall by a single broad muscular band, passing across the prostate glands to XIX. Where the vas deferens joins the prostatic duct, the latter is much dilated into a bulbous structure (bursa?). The penial setae are fairly

broad, flattened, the tip more so, and spatula-like, with a cochleariform depression. The ectal portion of the shaft ornamented with short clusters of sharp toothlets that are uniformly scattered, and which do not extend to the region of the tip. Length of mature seta mm; midshaft diameter 39  $\mu$ m (mean of 2). Ovaries, consisting of sheaves of oocytes, and small-medium funnels, present in XIII; ovisacs apparently absent. Spermathecae a single pair, in VIII, consisting of a large, sacciform ampulla and a copiously inseminated, digitiform diverticulum of similar length, their ectal ends fusing simultaneously into a short duct. Length right spermatheca of VIII = 1.6 mm.

### Remarks

As type specimens cannot be located, this species is erected on the illustration and account in Dyne (1984, unpublished) (ICZN 1999: Art. 73.1.4.). It was tentatively placed in *Rhododrilus* by Dyne.

*Kayarmacia cochlearis* exhibits a further elaboration of the dual male system in *Kayarmacia*, in having a bursa-like dilatation of the terminal portion of the prostatic duct, where the thickened vas deferens joins it.

### *Kayarmacia queenslandicus* (Michaelsen, 1916)

(Figs 137–139)

*Rhododrilus queenslandicus* Michaelsen, 1916: 4–6, pl. 1, fig. 9–11.

*Kayarmacia queenslandicus*; Jamieson 1997: 257–262, fig. 28–30, 39.

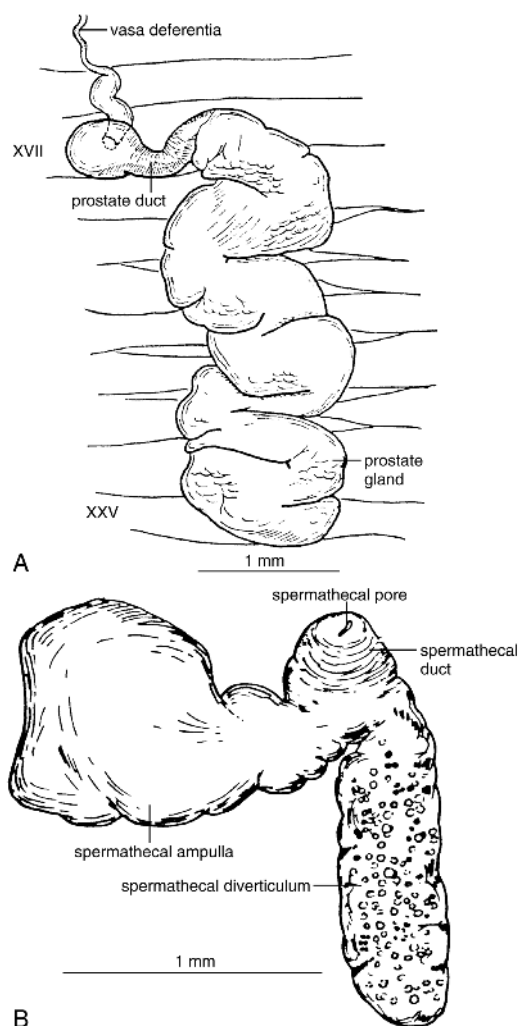
**TYPE LOCALITY:** Qld, ca 15°S, Cape York, banks of Alice River, a single much dissected specimen in two pieces, labelled 'Kap York, Mjöberg, Alice River'.

**SYNTYPES:** HM V8487.

**OTHER MATERIAL:** (Jamieson 1997) Qld, 15°27'45"S 142°10'12"E, Emu Lagoon, Alice-Mitchell Rivers National Park, altitude 22±2m, top-soil on sandy levee bank, open woodland, K.R. McDonald, 9 Feb 1993. ex QM Acc#2344, specimens 1–6 QM G213385.

### Description (after Michaelsen 1916; Jamieson 1997)

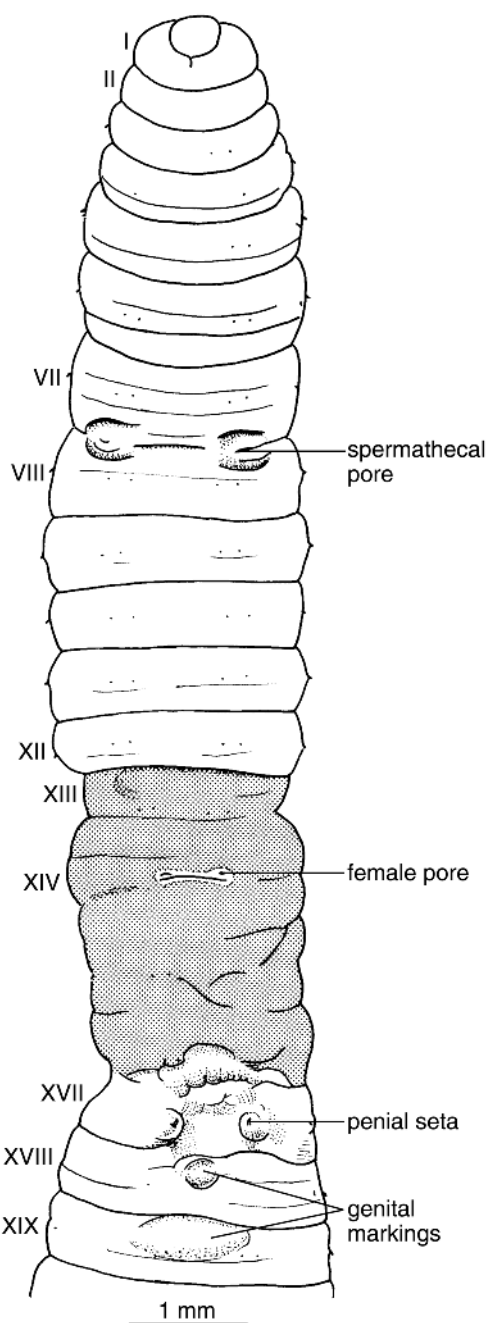
Length 49–75 mm. Width (midclitellar) 1.2–1.9 mm; greatest width (forebody) 2.3 mm. Segments 124–150. Pigmentless in ethanol; clitellum greyish buff. Prostomium epilobous, ca 1/4; small, broad and open. Peristomium approximately as long as segment II. Dorsal pores absent (Michaelsen 1916) but sporadically visible (Jamieson 1997) from shortly anterior to the clitellum (verified by exudation of alcohol when specimen is placed in water). Setae closely paired; in XII, *aa: ab: bc: cd: dd* = 6.6: 1.0: 6.1: 0.7: 26.1; or 13.6: 2.1: 12.5: 1.5: 54.2. Clitellum annular, XIII–XVI (Jamieson), –XVII (Michaelsen); setae normally developed. Male genital field: a deep transversely elliptical depression in XVII, preceded posteriorly in XVI by a midventral, transverse glandular elevation, and extending somewhat onto XVIII median to a pair of strongly protuberant combined male and prostatic porophores (in XVII), the median borders of which project ventromedially over the depression, the lateral borders of which are poorly distinguished from the lateral region of the segment; from the



**Fig. 136.** *Kayarmacia cochlearis* sp. nov., Holotype: A, right prostate; B, left spermatheca.

summit of each papilla, in setal line *a*, projects a penial seta. An indistinct hemispheroidal midventral genital marking present presetally in XVIII; a larger indefinite tumescence presetally in XIX, or a hemispheroidal midventral genital marking present post-setally in XVIII. Female pores a pair of deep punctuations very shortly anterior median to seta *a* of XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8, in *ab* (Michaelsen) or shortly lateral of *b*; each with a large approximately ellipsoidal epidermal elevation surrounding it which extends well laterally of *b* and to or median of *a* and is bounded anteriorly by a crescentic groove (Jamieson 1997).

Septa 5/6 or 6/7–8/9 the strongest, moderately strongly thickened. Dorsal blood vessel single, continuous on to the pharynx. Last hearts in XIII; those in X–XIII large and heart-like with large connective to the supra-oesophageal vessel and slender connective to the dorsal vessel; those in IX anteriorly slender, with dorsal connective only. Gizzard in V; large, strong, glossy, muscular though compressible. Oesophagus lacking calciferous glands; segmentally slightly swollen and vascularised in VIII–XVI, especially vascular in X–XIV or XI–XVI. Intestine commencing in XVII but not sharply demarcated from the oesophagus. Typhlosole absent. Holonephric. Nephridia of II, III and especially IV enlarged and much lobed though not truly tufted; connection to the gut not detected. Other nephridia with avascular ducts discharging anterior to the lateral setal couples, specifically in *c*. Large male funnels in X and XI, with spermatozoal iridescence. Seminal vesicles at maturity in IX and XII, racemose, much divided, those in XII the larger. Paddle-shaped ovaries in XIII. Prostates tubular, extending from XVII to XXIV; at maturity zigzagged; the duct extending from XVII–½XIX, with an abrupt bend in XIX; the short portion ental to the bend not noticeably muscular, the remaining, more ectal portion forming a wide, muscular, glossy tube extending forwards towards the male porophore; vasa deferentia on each side fused, slender into the anterior portion of XVI; in posterior XVI and XVII forming a muscular tube of similar appearance to the prostate duct but slightly wider and approximately U-shaped (ejaculatory duct) (Jamieson, see Remarks below). Penial seta ca 0.96 mm (Jamieson) to 1.2 mm (Michaelsen) long; one (Jamieson) or two (Michaelsen) on each side; the tip curved in a hook as in *K. adelphicus*, extending from XVII into anterior XIX; the curved apical portion ornamented 'dorsally' and 'ventrally' by extensive finely toothed transverse rows but the sides smooth; the ventral tooth rows linked up transversely so as to straddle much or the whole of



**Fig. 137.** *Kayarmacia queenslandicus* (Michaelsen, 1916), genital field of QMG 213385.

[From Jamieson 1997]

the ventral surface (Jamieson). Michaelsen described the penial setae as follows: 2 per follicle, about 1.2 mm long, about 50  $\mu$ m at midlength, distally gradually becoming thinner, the end simple and sharply pointed, proximally somewhat thicker, reaching ca 80  $\mu$ m; distal third very strongly curved, approximately at right angles, proximal end rather to very strongly bent in the same direction; the middle region slightly convex laterally; the concave side of the distal end with an almost blade-like flattening and almost comma-shaped in cross section; interior of the seta with a delicate and sparse oblique longitudinal striation; the distal end ornamented with two rather large longitudinal rows of irregular and finely toothed transverse rows, one on the convexity the other on the concavity; the two rows separated laterally by a narrow smooth zone; those on the convex side extend almost to the distal tip; those on the concave side end well before the beginning of the

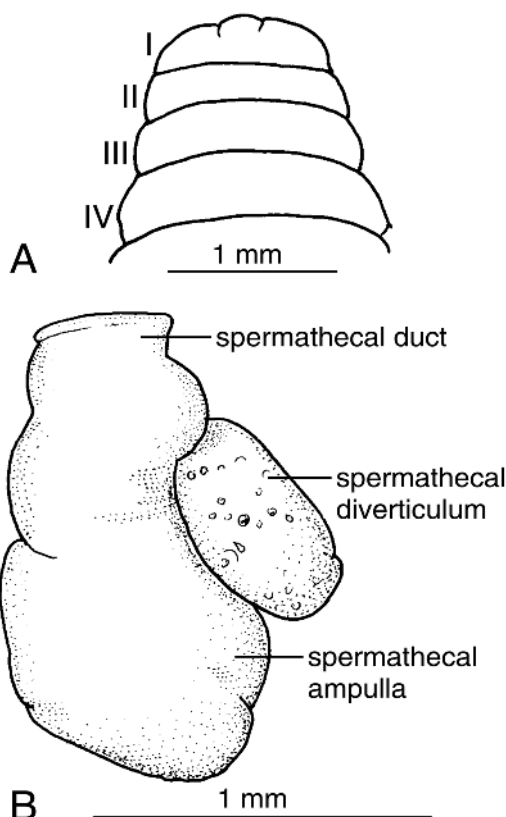
blade-like region, though extending almost to the distal fourth of the seta; transverse rows clearly visible at the distal border as scoop-like raised area. Spermathecae a pair in VIII, opening at the anterior border, each with a large ovoid ampulla, the duct of which consists of three regions in longitudinal succession: an ental third which is approximately tubular and is well demarcated from the ampulla, a swollen intermediate region which receives the diverticulum, and an ectal third which forms a wide, short, muscular, tubular duct. Diverticulum elongate-ellipsoid, with numerous nacreous sperm masses which possibly represent non-protuberant sperm chambers, and with a narrow connection to the spermathecal duct. Length left spermatheca = 1.5 mm; length ampulla = 0.9 mm; ratio length spermatheca: length duct = 2.5; length diverticulum = 0.7 mm.

### Remarks

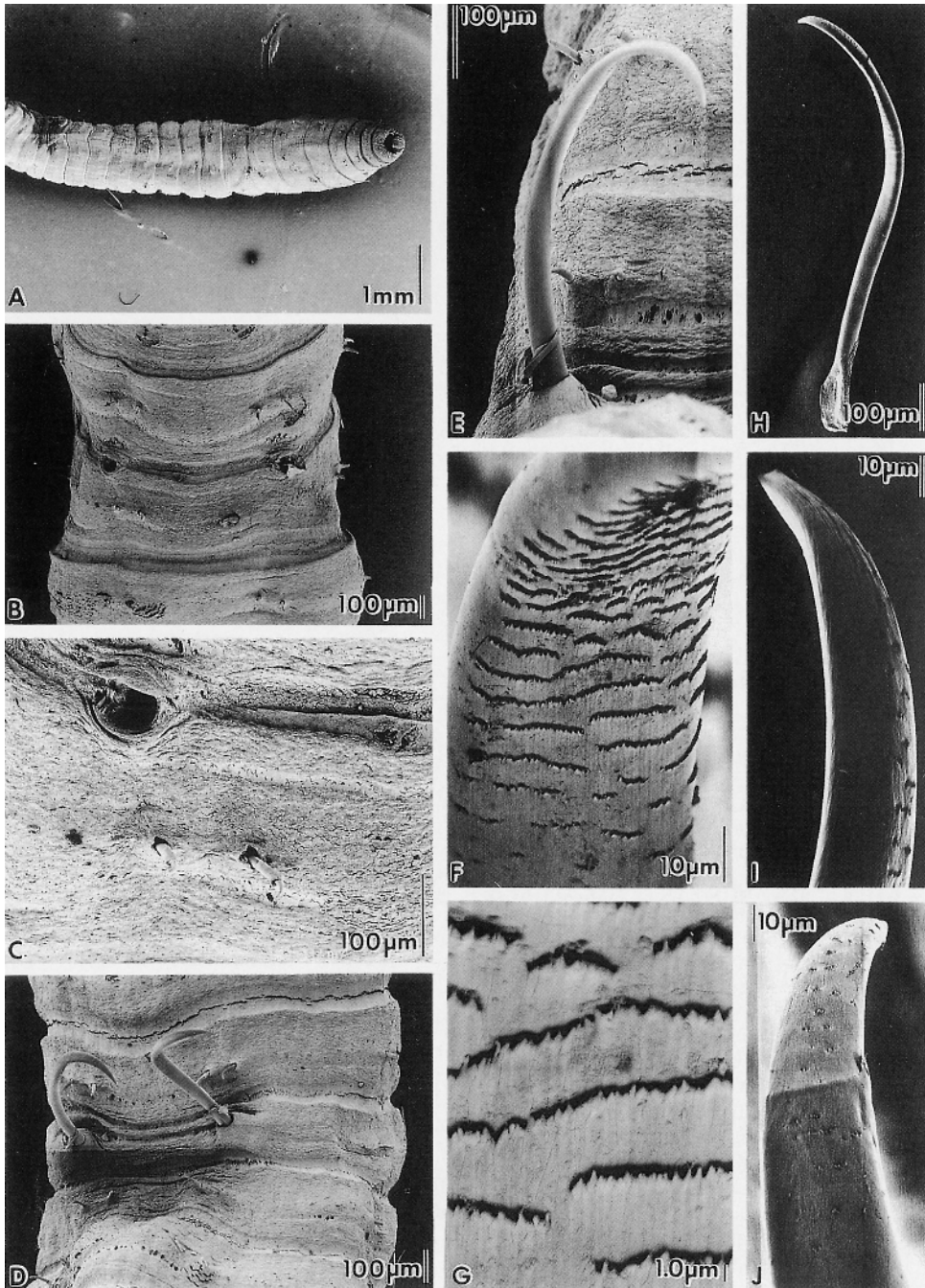
The type locality is the Alice River, which Michaelsen (1916) wrongly thought to be a tributary of the Coleman River. Michaelsen's material was collected from the banks of the river but he recognised it as at least potentially 'limnische Lebensweise'. The stated absence of dorsal pores would correlate with an amphibious existence. The water table is at the surface and in the rainy season most of the area, excepting the levee banks, is covered by water (K.R. McDonald, pers. comm.). However, in the newer, Emu Lagoon material, dorsal pores were sporadically demonstrable though possibly vestigial.

The type material in the Hamburg Museum (HM V8487) examined by the second author some decades ago consisted of a postclitellar region and a much-dissected portion of body wall anterior to segment XIII with some appended organs. The left spermatheca remained, with a swollen duct and single clavate diverticulum. The other portion had an attached tubular prostate lacking the ectal duct. The nephridia had conspicuous, fairly wide, ectal ducts but no bladders.

Identification of the Emu Lagoon material as *Kayarmacia* (= *Rhododrilus*) *queenslandicus* was based on close morphological similarity and collection near the type locality. The identification appears to be confirmed by the unusual ornamentation of the penial setae in which transverse rows of scales are present dorsally and ventrally on the apical curvature but the sides are smooth. Michaelsen's description of *Rhododrilus queenslandicus* accords closely to that of the Emu Lagoon material but some points of disagreement require mention. The clitellum is said to occupy XIII–XVII, in XIII and posterior XVII being less well developed, whereas in the Emu Lagoon specimens it ends with segment XVI. No accessory



**Fig. 138.** *Kayarmacia queenslandicus* (Michaelsen, 1916), QMG 213385: **A**, dorsal view in region of prostomium; **B**, right spermatheca. [From Jamieson



**Fig. 139.** *Kayarmacia queenslandicus* (Michaelsen, 1916), Emu Lagoon specimen QMG213385: **A**, ventral view; **B**, region of spermathecal pores; **C**, a right spermathecal pore; **D**, penial setae *in situ*; **E**, right penial seta *in situ*; **F**, ornamentation of penial seta; **G**, same at higher magnification; **H**, penial seta of specimen 2; **I**, dorsal ornamentation of a penial seta of the same; **J**, dorsal ornamentation of a penial seta of specimen 6. [From Jamieson 1997]

genital markings were present. The thickened end of the male duct was shown to open into the prostate, a condition that Michaelsen confirmed by sectioning, whereas in the Emu Lagoon material these two ducts were shown to be closely apposed at the male pore but actual fusion was not demonstrated. Michaelsen reported two penial setae for each follicle in the type-material whereas one only is present on each side in the Emu Lagoon material. Although the description of the spermathecae given by Michaelsen differs in some regards relative to the Emu Lagoon material, the differences are doubtfully significant and his illustration agrees well with that for the latter; the very wide spermathecal duct illustrated for the type corresponds with the wide middle region of the duct in the new material. In view of the close similarities of the Emu Lagoon material with the types, including the ventral ornamentation and smooth sides of the setal curvature, these

differences of description do not appear to merit specific separation. Setal ratios measured by Jamieson (1997) for the type material differ in some respects from the Emu Lagoon material but the significance of the differences is uncertain. The type ratios, for XII, are:  $aa: ab: bc: cd: dd = 3.2: 1.0: 4.5: 0.8: 15.2$  or  $10.6: 3.8: 14.1: 1.9: 50.0\%$ .

The close similarity of *Kayarmacia queenslandicus* and *K. adelphicus* is discussed in the account of the latter. The Emu Lagoon specimen of *K. queenslandicus* in which the genital marking in XVIII is postsetal, as in *K. adelphicus*, further narrows the gap between the two taxa. If genital setae were found in *K. queenslandicus* retention of *K. adelphicus* as a distinct species would still be supported by the difference in ornamentation of the penial setae.

*Microsclex* Rosa, 1887

*Microscolex* Rosa, 1887: 1.

**TYPE SPECIES:** *Lumbricus phosphoreus* Dugès, 1837 (circummundane).

*Eudrilus?*; Fletcher 1887: 378.

*Microscolex* (part.); Michaelsen 1900: 139; Pickford 1937: 42; Lee 1959: 95.

*Microscolex* + *Notiodrilus*, excluding *Diplotrema*; Jamieson 1971b: 102–103; 1974b: 38; Jamieson and Dyne 1976: 447–449.

**Diagnosis (after Rosa 1887; Jamieson 1971b; Jamieson and Dyne 1976)**

Setae 8 per segment; *dd* typically less than 30% of the circumference. Genital setae absent; penial setae present. Prostates 2 pairs, their pores on XVII and XIX, or 1 pair on XVII. Male pores 1 pair, on XVII or XVIII, rarely fused with the anterior prostatic pores. Spermathecal pores 2 pairs, in 7/8 and 8/9, or 1 pair in 7/8 or 8/9; rarely (*M. dubius*) absent. Last hearts typically in XII. Nephropores a single series on each side.

at least after a few anterior segments. Extramural calciferous glands absent or present (*M. dubius*). Gizzard reduced or rudimentary, sometimes well developed. Holandric, or proandric with or without rudimentary funnels in XI. Testis-sacs absent. Nephridia with simple ovoid, pear-shaped or tubular, never J-shaped, terminal vesicles.

## Distribution

Southern South America; Falkland Islands; South Georgia; Kerguelen; Marion Island; South Africa; Campbell Island; Auckland and Antipodes Island. Macquarie Island. Darien (?). Two species (below) circummundane.

## AUSTRALIAN SPECIES

1. *Microscolex* (?) *dubius* (Fletcher, 1887)  
(*Eudrilus*) (circummundane).
2. *Microscolex macquariensis* (Beddard, 1896)  
(*Acanthodrilus*) (Macquarie Island).
3. *Microscolex phosphoreus* (Dugès, 1837)  
(*Lumbricus*) (circummundane).

## KEY TO AUSTRALIAN SPECIES OF *MICROSCOLEX*

- |       |  |                         |
|-------|--|-------------------------|
| 1     | a. Male pores and one pair of prostatic pores close together or united on XVII . . . . . | 2                       |
|       | b. Male pores on XVIII. Two pairs of prostatic pores on XVII and XIX . . . . .           |                         |
|       |  | <i>M. macquariensis</i> |
| 2(1a) | One pair of spermathecae and pores present . . . . .                                     | <i>M. phosphoreus</i>   |
|       | Spermathecae absent . . . . .  | <i>M. dubius</i>        |

### Remarks

Consideration of the status of *Microscolex* requires discussion of *Notiodrilus*. *Notiodrilus* was suppressed in *Microscolex* by Michaelsen (1905) because he discovered two morphologically similar species, one of which had the male pores and single pair of prostatic pores on XVII (the microscolecin arrangement), as in *Microscolex*, whereas the other had male pores on XVIII and two pairs of prostatic pores, in XVII and XIX (the acanthodrilin arrangement). Pickford (1932) found a similar variation to occur intraspecifically in *Microscolex georgianus* (Michaelsen, 1888), the type-species of the former *Notiodrilus*. She reserved the genus *Microscolex* for species with

ovoid or pear-shaped nephridial bladders whether microsolecin or acanthodrilin. *Notiodrilus* was accepted as its junior synonym.

Jamieson (1971b) reinstated *Notiodrilus* as a subgenus of *Microscolex*. Widening of the interval *ab* behind the male pores, which are combined with a single pair of prostatic pores in XVII (the microscolecoid condition), seen in *Microscolex phosphoreus* (and *M. dubius* and *M. beddardi*) was used by Jamieson (1974b) to diagnose the subgenus *Microscolex*. Michaelsen (1900b) had already noted the corresponding contraction of *ab* in the vicinity of the male pores as a characteristic of *Microscolex*. *Notiodrilus* was defined by Jamieson (1974b) as a subgenus lacking the post-genital widening of *ab*. Pending clarification of

their true relationships, *Notiodrilus* accommodated all non-Australian species of *Eodrilus*. *Notiodrilus* therefore contained species with and without nephridial bladders. The third subgenus, *Diplorema*, was defined by the presence of spermathecal genital setae, though absence of these, deduced to be by loss, was later demonstrated for a few compatriot species (Jamieson and Dyne 1976). *Diplorema* was restored to generic rank by Dyne (1987) and its generic status has continued to be recognised (Jamieson 1997; Dyne and Jamieson 1998).

Dyne (1984, unpublished) retained the corresponding contraction of intersetal interval *ab* in segments in the vicinity of the male pores as a distinguishing feature of the subgenus *Microscolex* but recognised that many additional, acanthodrilin and microscolecin, species show this feature: *M. aucklandicus* (Benham, 1903), *M. bovei* (Rosa, 1889), *M. campbellianus* (Benham, 1905), *M. collislupi* Michaelsen, 1910), *M. crozetensis* (Michaelsen, 1905), *M. enzanspergeri* (Michaelsen, 1905), *M. kerguelarum* (Grube, 1877), *M. luisae* (Michaelsen, 1899), *M. macquariensis* (Beddard, 1896). Examination of material of *M. macquariensis* obtained by Jamieson from Macquarie Island confirmed narrowing of setal interval *ab* towards the male pores, from behind and in front (see Jamieson and Dyne 1976). In addition to the type-species, *Notiodrilus georgianus*, the subgenus *Notiodrilus* contained *N. albus* (Beddard, 1895a), *N. magellanicus* (Beddard, 1895a), *N. occidentalis* (Beddard, 1895a), *N. philippi* Michaelsen, 1900a, and *N. purpureus* (Beddard, 1895a).

It is here noted, in conflict with this convenient subdivision, however, that *Microscolex macquariensis* had been found by Jamieson and Dyne (1976) to be exceedingly close morphologically to the type-species of *Notiodrilus*, *N. georgianus* (Michaelsen, 1888), resemblance including not only the vesiculate condition with spherical nephridial bladders [discharging shortly below *c* lines in *N. georgianus* and almost imperceptibly below *c* in *N. macquariensis*], but also characters of a near-specific nature such as genital markings on segment X. Furthermore, in the illustration of *Notiodrilus georgianus* posteriad contraction of *ab* occurs at least in front of the male genital pores (Jamieson 1974b; segments behind XX are not illustrated).

Thus, distinction of *Microscolex* from typical *Notiodrilus* is uncertain especially as variation from the acanthodrilin to the microscolecin condition can occur intraspecifically, as already noted, in '*Notiodrilus*' *georgianus* by Pickford (1932). In the present work *Notiodrilus* is

therefore provisionally suppressed in *Microscolex* pending a wider revision of the Acanthodrilinae. The type-species of both *Microscolex* and *Notiodrilus* are vesiculate and separable by this condition from *Diplorema*. Neither taxon has the spermathecal genital setae usual in *Diplorema*. The the large numbers of avesticulate extra-Australian acanthodriline worms in South Africa and elsewhere are mostly attributed to *Eodrilus*.

Following the re-assignment to *Diplorema* of *Eodrilus cornigravei*, the type-species of the genus *Eodrilus*, by Jamieson (1971a), some 35 species were unplaced until tentatively absorbed into the subgenus *Notiodrilus* of *Microscolex sensu* Jamieson (1974b). The characterisation of *Eodrilus* by Pickford (1937) that gained wide acceptance (e.g. Gates 1967, Lee 1959) was based on the negative and probably plesiomorphic feature of a lack of nephridial vesicles. It was not surprising, then, that the genus became the repository of a large number of acanthodriline species from disparate parts of the globe. The reassignment of these (with the exception of those possessing genital setae) to *Microscolex* (even within a subgenus *Notiodrilus*) is, as Dyne notes, clearly unsatisfactory, as it fails to convey the fact that there exist a number of geographically isolated species-groups with independent evolutionary courses. Dyne observes that both the South African and New Zealand components, for instance, are respectively homogeneous; for instance, all New Zealand forms share the unusual and apomorphic bifurcate condition of the dorsal blood vessel (though we may add, this duplication also occurs in *Microscolex macquariensis*, and in some *Diplorema* species). Other taxonomic discrepancies can be compiled, such as the universal presence of penial setae in the South African species as opposed to their absence (with one exception) in New Zealand forms. It may be possible to segregate within the extra-Australian '*Eodrilus*' congeries, a number of species-groups or genera advancing along quite separate selectional lines. Even by conventional taxonomic standards, neither the South African nor New Zealand '*Eodrilus*' groups is closely linked with the southern South American forms (recognised by Dyne 1984, unpublished, as *bone fide* *Microscolex* (*Notiodrilus*) and, if vesiculate, here provisionally placed in an undivided *Microscolex*). It is here noted that the setae are widely paired in the type-species of both *Microscolex* and *Notiodrilus*, as can be seen also in *Microscolex macquariensis* (Fig. 142). In contrast, both the New Zealand and African '*Eodrilus*' species, the setal couples are closely paired; moreover, the general



configuration of the male fields and prostatic arrangements, positioning of penial setae, etc. are dissimilar in the three groups.

An essentially similar case for independent generic recognition has been argued by Dyne for the holonephric Central American '*Eodrilus*'. Some of these have developed calciferous glands, and have thus clearly diverged from the ancestral acanthodrilid line; others exhibit ecological and morphological peculiarities unknown in the southerly '*Eodrilus*' forms (e.g. the cavernicolous *E. mexicanus* Gates, 1967, which is apparently hologynous). The apparently closely related genera *Balanteodrilus*, *Zapotecia* and *Neogaster* (part. -*divergens* only?) can be regarded as species-groups exhibiting more obvious modifications of the ancestral morphology.

No evidence exists to suggest that '*Eodrilus*' species have either the capability for trans-oceanic dispersal, or, like certain pheretimoids, the ability to exploit a large range of habitats. The apparent restriction of South African '*Eodrilus*' species to the coastal belt of the south and south-west Cape observed by Pickford (1937), rather than necessarily indicating a short establishment time in South Africa, could equally well be interpreted in terms of ecological and climatic preferences.

On the other hand, there is strong evidence that the present circum-Antarctic distribution of *Microscolex sensu lato* is a comparatively recent phenomenon, rather than illustrating, as Omodeo (1963) suggests, a fragmented range across pre-drift Gondwanaland. Many of the islands and other land-masses involved have either been submerged in the interim (e.g. Macquarie Island during the Miocene, see Jamieson 1974a), or subject to extensive glaciation (e.g. southern tip of South America, including Tierra del Fuego, during the Pleistocene), thus necessitating a somewhat recent recolonisation. The well-documented euryhaline tendencies and peregrine abilities of some members of the genus are certainly not inconsistent with this concept. Detailed re-examination of some of the lesser-known species may place them within the ambit of the *M. dubius*/*phosphoreus* complex. For instance, Gates (1972) suggests that *M. luisae* could well be interpreted as a quadriprostatic morph of *M. phosphoreus*. Furthermore, the athecate *M. beddardi* may be a pro-andric morph of *M. dubius* (see Jamieson 1974b).

We support the contention of Michaelsen (1905, 1911) (who also argued for a modern dispersal of *Microscolex*, mostly through the agency of the West-Wind Drift) that the ancestral 'home' of *Microscolex* was the southern end of South

America. It is there that the greatest concentration of species of both *Microscolex* (including *Notiodrilus*) and the closely related *Yagansia* occur. The objections raised by Benham (1909), that 'rafting cocoons of would-be colonisers must invariably be dashed to pieces against the shores of potentially habitable islands, or engulfed (sic) by whales' warrant little consideration, and are ably refuted by Michaelsen (1911).

### ***Microscolex dubius* (Fletcher, 1887)**

(Figs 140, 141)

*Eudrilus? dubius* Fletcher, 1887: 378.

*Microscolex dubius*; Michaelsen 1899: 97; Michaelsen 1907: 146; Pickford 1937: 429–432, figs 398–399; Omodeo 1948: 1–6; Gates 1972: 34–35.

**TYPE LOCALITY:** NSW, 35°59'S 146°00'E, Mulwala, Sydney; SA, Adelaide.

**SYNTYPES:** [NSW material] presented by Fletcher (Nov. 1924), catalogued as 'syntypes?', AM W 1360. [SA material] many specimens, presented by Fletcher (Nov. 1924, collected 1895), catalogued as 'syntypes?', AM W1361.

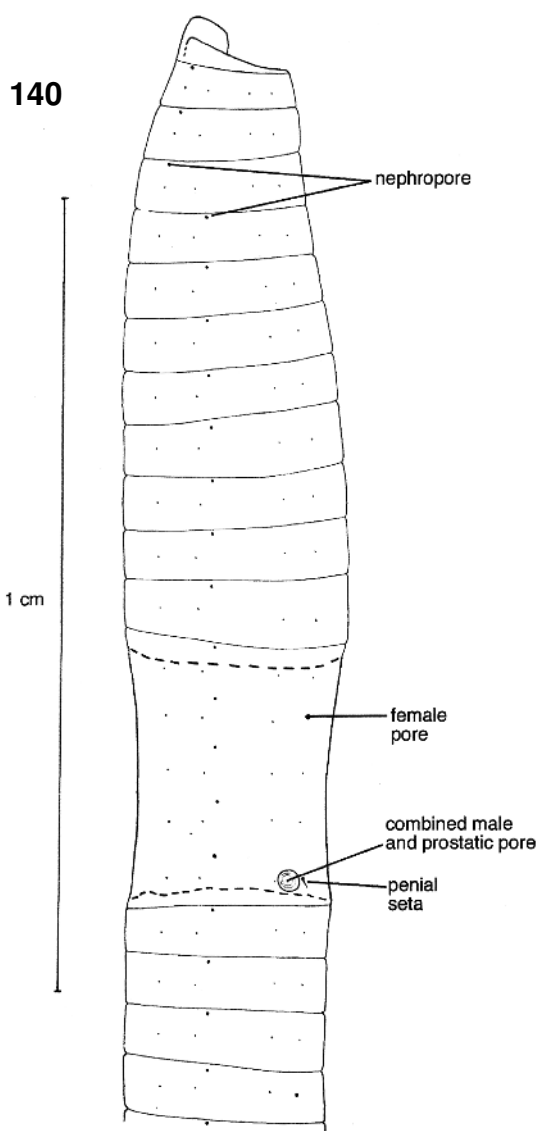
**FURTHER RECORDS:** Much additional material of this species from widespread localities in NSW is present in the Australian Museum, Sydney: AM W1404; 2391; 2475; 2566; 2570; 2790; 2792; 2800; 2804; 2805; 2988; 3002; 3037; 3321; 3342; 3349; 3436; 197265; 197266; 197267; 197268; 197269; 197270; 197271; 197272; 197273; 197274; 197275; 197276; 197277; 197278; 197279; 197280; 197281; 197282; 197283; 197284. ACT: 35°19'S 148°56'E, Cotter Dam, Canberra, Coll. and ident. E. Easton, 1983, AM W21732; 35°17'S 149°13'E, coll. and ident. 25 Aug 1942, W. Boardman (presented March 1943), AM W3352. SW WA Narragon, coll. S Lannach, ident. E. Easton 1983, W 197324; Travellers Inn Motel, Esperance, coll. (and ident.) I. Abbott, AM W199102; 70 km N of Esperance, 8 km S of Grass Patch, coll. and ident. I. Abbott 13 Aug 1980, AM W199103–199104; 75 km W of Ravensthorpe, out of Esperance, coll. (and ident.) I. Abbott 16 Aug 1980, AM W199106; Ward Street, Kalgoorlie, coll. J. Rooney 13 Aug 1980, ident. I. Abbott, AM W199107; "Glenbourne", near Ellen Brook, coll. (and ident.) I. Abbott 10 Jul 1982, AM W199142; S of Wonga Hills, B. Davey's farm, coll. (and ident.) I. Abbott, 07 Sep 1983, AM W199143; W of Mt Barker, F and B Lynch's farm — pasture, coll. C.A. Parker, Sep 1982, ident. I. Abbott, AM W199144.

Also recorded from Tasmania (Blakemore 2000).

**Description (after Fletcher 1887; Pickford 1937; Omodeo 1948; Gates 1972)**

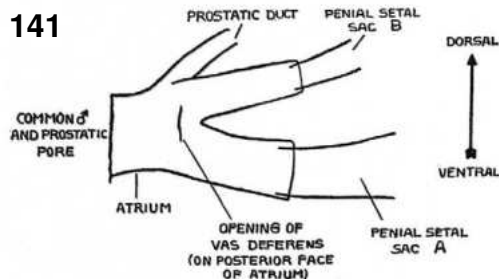
Length 30–102 mm. Segments 111–117. Unpigmented. Epilobous, open. Dorsal pores absent. Nephropores in *c*–IV where they are in *d* lines. Clitellum annular, XIII, 1/nXIII–XVI, i/nXVII. Setae widely paired but *ab* gradually narrowed through clitellum and onto XVIII, gradually widening through XIX–XXV;  $ab < cd < bc$   $ca = aa$ ;  $dd < \frac{1}{2}u$ . Spermathecae and their pores absent. Female pores slightly anteromedian of setae *a* of XIV. Pores of a common atrium ('small invagination' sensu Gates, 1972) of male and prostatic pores a pair on XVII, on papillae, in *ab*; penial setae *a* and *b* protruded through the pore.

Septa 6/7–13/14 slightly thickened. Gizzard rudimentary, in V. Intestine commencing in XVI; typhlosole absent. Dilatations of the oesophagus in IX–XV were considered by Omodeo (1948) to constitute Morren's (calciferous) glands and to contain calcareous concretions. Dorsal vessel single; last hearts in XII. Nephridial vesicles ocarina-shaped posteriorly, with pointed ends medially and with short ducts from ventral side laterally (with well-developed parietal sphincters?). Holandric; seminal vesicles two pairs, in XI and XII. Ovaries fan-shaped, with several egg strings. Ovisacs small, lobed. Prostates one pair, each restricted to one segment, ental end sometimes coiled in an inrolled spiral; duct short, the ectal part not more strongly muscularised than the ental part. The prostate duct unites with the follicle neck of penial seta *b* just as this enters the atrium; the opening of the common vas deferens lies on the posterior face of the atrium midway between the mouths of the two penial setal follicles; the vas deferens passes laterally between the prostatic duct and the body wall, just behind the prostate duct it bends at right angles and, running parallel to it, enters the atrium on its posterior face (Pickford 1937). Penial setae of the *a* and *b* 35  $\mu$ m, thickness ca 26  $\mu$ m.



**Figs 140, 141, *Microscolex dubius* (Fletcher, 1887).** 140, lateral view of anterior region; 141, diagram of a cuticle preparation from the region of the right prostatic pore of a semi-mature specimen from Hout Bay, S Africa, showing the union of the prostate duct with the neck of penisetal sac *b* and the common atrium into which the penisetal sacs and vas deferens open.

[140, modified after Bouché 1972: 671;  
141, from Pickford 1937].



**Remarks**

This species is circummundane but is considered to have originated in southern South America. This view was adopted before Australia was known to have a large acanthodrilid fauna but the widespread occurrence of *M. dubius* in Australia, as elsewhere, gives support to regarding it as an introduction and/or invader. Gates argues for regarding it as possibly a parthenogenetically degraded descendant of *M. phosphoreus*. It appears to differ from *Microscolex phosphoreus* in having a common male and prostatic atrium on each side, in lacking spermathecae and apparently (review by Gates 1972) in not exhibiting bioluminescence.

In view of the apparent very close relationship of *M. dubius* to *M. phosphoreus* the reported absence of luminescence in the former species has been puzzling. It is of interest, therefore, that Blakemore (2000) states, in reference to Tasmanian material of *M. dubius*, that 'it does not however give as phosphoresce response'.

***Microscolex macquariensis*****(Beddard, 1896)**

(Figs 142–145)

*Acanthodrilus macquariensis* Beddard, 1896: 208.*Notiodrilus macquariensis*; Michaelsen 1900b: 130.*Acanthodrilus macquariensis*; Benham 1901: 132–133.*Notiodrilus macquariensis*; Benham 1903: 276–277, 1909: 275; Cognetti de Martiis 1906: 1–72.*Microscolex macquariensis*; Michaelsen 1907: 143; Pickford 1937: 593; Lee 1959: 101–103.**TYPE LOCALITY:** Macquarie Island, 54°30'58"S 158°55'23"E..**SYNTYPES:** BM(NH) 1904.10.5.873–6.

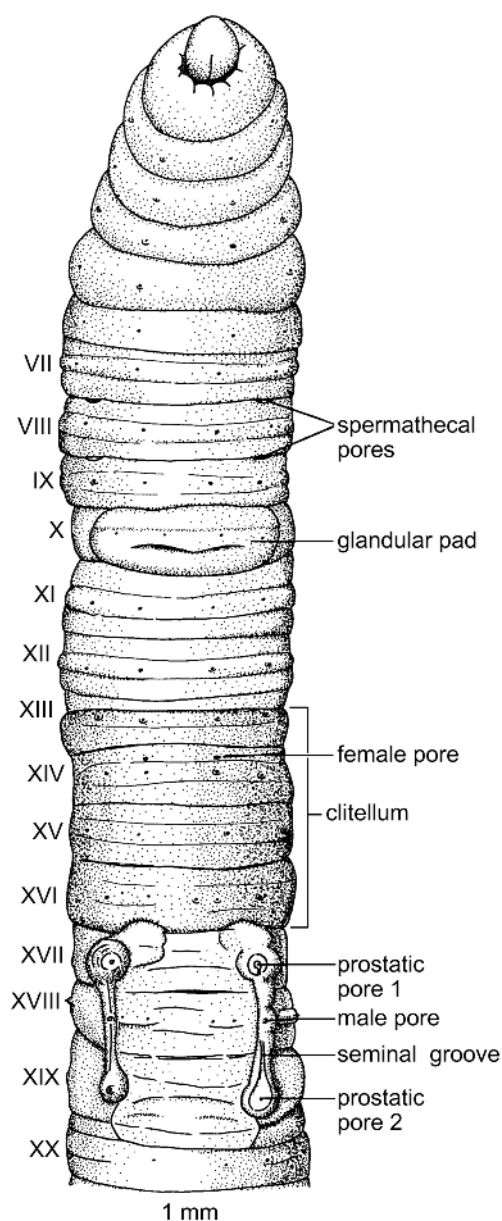
**OTHER MATERIAL:** Macquarie Island. Six specimens. Coll. Pres. Aust Ant Exp Public Comm (Jan 1923), I dent. W. B. Benham, AM W967; same, 3 specimens, AM W968; Macquarie Island, Lake Scoble area, in water-logged peat. Coll. A. Evans, 11 March 1963, ident. B.G.M. Jamieson, 5 clitellate specimens, described here.

**Description (after Beddard 1896; Lee 1959; Jamieson, unpublished)**

Length 25 (Beddard 1896), 35–36 mm. Width (forebody) = ca 2 mm (present study)–4.6 mm (Lee 1959). Segments 85 (Lee 1959)—100 (Beddard 1896). Prostomium epilobous (Beddard 1896; Lee 1959). Setae widely paired, the ventral

setal couple, *ab*, contracting to closely paired in the region of the prostatic pores and widening again posterior to these; setae *a* and *b* absent in XVII and XIX, always present in XVIII; a dark speck which may be visible in XVII or XIX at locus *a* consists only of diffuse brownish material and is not a seta; *aa: ab: bc: cd: dd* = 1.1: 1.0: 1.2: 1.4: 2.6: 10.9 in IX, = 1.7: 1.0: 1.5: 1.7: 3.0: 13.2 in XXV; *dd: u* = 0.24, 0.23, respectively (mean of 5 specimens, present study). Clitellum annular, ½XIII–XVI (Beddard 1896; specimens 1, 3, 4, present study) XVII (specimen 2; variation in Lee 1959); in longitudinal sections of specimen 5 it occupies XIII–½XVI ventrally and ½XIII–½XVII dorsally. Prostatic pores 2 pairs, in XVII and XIX; in *b* lines (present study; Beddard 1896; cf *a* lines, Lee 1959) relative to preclitellar segments and those behind XX, on circular papillae which are interconnected on each side by a straight or slightly laterally bowed seminal groove with prominent borders. Male pores (specimens 1 and 4) in the seminal grooves lateral of the persistent ventral setal couples which are closer together here than in neighbouring segments. Nephropores a single series in *c* lines (confirmation). Female pores presetal in XIV anterior to (Lee 1959) or very slightly lateral of (present study) setae *a*. Accessory genital markings: a transverse unpaired pad filling the length of X and extending lateral of *b*, bearing the ventral setal couples; with two conjoined crescentic postsetal depressions (specimens 1 and 5); a suggestion of a transverse pad postsetally in XIX (specimen 1); a similar pad in XII and a unilateral pad on the right, centred on *ab*, in X, all with sucker-like transverse clefts in *ab* (specimen 2); slight tumescences with depressed centres in *ab* lines, extending from the setal arc posteriorly in X (paired, XI (left) and XII (right) (specimen 3); two pads in *ab* of X, each with a transverse depression, just including the setae *ab* anteriorly (specimen 4); therefore, genital markings tumescences in some or all of X, XI and XII, paired or unilateral, or medially conjoined (present study); paired tumescences in X or XI, sometimes absent (Beddard 1896). Spermathecal pores 2 pairs, in 7/8 and 8/9, in *b* lines (present study; Beddard 1896; Lee 1959); small slits, not on papillae (specimen 1), or with tumid whitish lips (specimen 2).

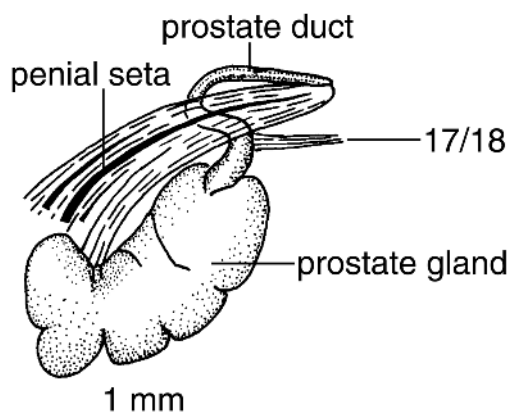
No septa strongly thickened; from longitudinal section of specimen 5, 6/7–11/12 thicker than succeeding septa, with 9/10–11/12 the thickest but still only moderately thickened. Dorsal blood vessel at first single on the oesophagus but intrasegmentally paired posterior to 10/11 (Lee 1959) or after the first few segments of the intestine (present study). Hearts in X, XI and XII



**Fig. 142.** *Microscolex macquariensis* (Beddard, 1896). Genital field of a specimen collected by A. Evans on Macquarie Island in 1963.

[Jamieson 1965, unpublished]

(confirmation of Beddard 1896); absence from XIII confirmed in sections of specimen 5 (present study), contrary to X–XIII (Lee 1959). Pharynx large with dorsal diverticulum (sections). Oesophagus long and moniliform, not wide, intersegmentally constricted; vascular, especially

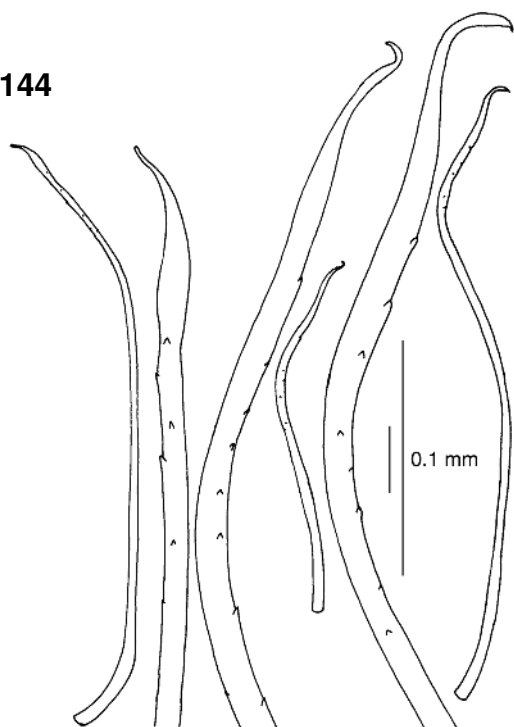


**Fig. 143.** *Microscolex macquariensis* (Beddard, 1896). Left anterior prostate gland of a specimen collected by A. Evans on Macquarie Island in 1963.

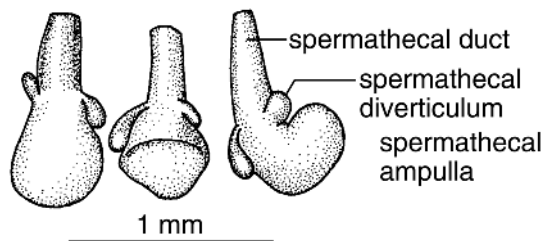
[Jamieson 1965, unpublished]

in XI; lacking diverticula or glands. Gizzard rudimentary or absent. Intestinal origin poorly defined; chloragogue thick on XVII; walls not thin until XX (through peristalsis?) but thicker and internally ridged in a few segments behind this; typhlosole absent. Sections reveal that the gut lumen is ciliated in XV and XVI, but not further anteriorly, nor in XVII posteriad, confirming commencement of the (unciliated) intestine in XVII. Intestinal contents include numerous filamentous green algae. Lymph glands, posterior diverticula of the septa, filled with coelomocytes, present in the intestinal region. Holonephric; vesiculate nephridia discharging in front of setae *c*; seen as far forward as IV; subspheroidal bladders with convoluted muscular walls. Holandric; seminal funnels free in X and XI; lined by spermatozoa in sections of specimen 5. Seminal vesicles racemose, in XII (specimen 1) or XI and XII (sections). Vasa deferentia ciliated. Prostates 2 pairs, in XVII and XIX; compact, limited to one segment; soft in texture and deeply divided by transverse furrows; ducts entally flaccid and bladder-like but for the greater part of their length narrow, of uniform thickness and with muscular sheen, the muscular duct forming a loop with its convexity directed laterally; this looped portion hidden under the corresponding penisetal follicle of which there is one to each prostate duct (specimen 1, present study). Longitudinal sections of the prostates (specimen 5) reveal that the glandular portion of each prostate has a tall lining

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**Figs 144, 145, *Microscolex macquariensis*** (Beddard, 1896), specimen collected by A. Evans on Macquarie Island in 1963. **144**, penial setae of left anterior follicle, each seta is shown whole and at its ectal end; **145**, spermathecae. [Jamieson 1965, unpublished]

epithelium surrounded by several layers of secretory cells; the lumen with its epithelium constitutes approximately one third of the thickness of the gland; there is a central lumen to the gland but this sends irregularly spaced ductules into the lining epithelium (tubulo-racemose condition); ciliation absent. Penial setae penetrating the parietes at the prostatic pore;

slender somewhat sinuous, with tip slightly hooked or recurved; the ectal region ornamented with sparse simple, triangular teeth (Beddard 1896; present study) or tubercles (Lee 1959) which in places give the profile a notched appearance; length of longest seta 0.9 mm, maximum width (near tip) 13  $\mu$ m (present study). Ovaries and funnels in XIII; in sections the ovaries have several egg strings; funnels are present in XIII but there are supernumerary female funnels in XII (vestigial hologyny); oviduct is ciliated. The accessory genital markings have a thickened epidermis but the musculature is not thickened (sections). Spermathecae 2 pairs, in VIII and IX, with large ampulla and straight stout duct of approximately equal length; 2 small clavate diverticula, bilateral (confirmation), at ental end of duct. A most unusual feature for Megascolecidae, is presence of spermatozoa in the ampullae but not in the diverticula (sections).

#### Remarks

The above account is based chiefly on notes and drawings (Jamieson 1965, unpublished) from material collected by A. Evans on Macquarie Island in 1963, but also reviews the type description of Beddard (1896) and the summary description of Lee (1959). Lee, with Benham (1909), states that the last hearts are in XIII but the type description (Beddard 1896) and the present study find the last hearts to be in XII. Accessory genital markings are not mentioned by Lee (1959) but their distribution given by Beddard (1896) falls within the configuration described here. Contraction of the ventral setal interval, ab, in the vicinity of the prostatic pores was also noted by Beddard (1896) and is typical of *Microscolex*.

#### *Microscolex phosphoreus* (Dugès, 1837) (Figs 146, 147)

*Lumbricus phosphoreus* Dugès, 1837: 17, 24.

*Microscolex nova zelandiae* Beddard, 1893: 33.

*Microscolex phosphoreus*; Michaelsen 1900b: 141; Michaelsen 1907: 148; Pickford 1937: 433–436, figs 400–404; Lee 1959: 103–104; Gates 1972: 35–37; Bouché 1972: 183–185; Sims and Gerard 1999: 140, fig. 50.

**TYPE LOCALITY:** France, Greenhouses, Jardin des Plantes, Montpellier.

**TYPES:** Lost.

**AUSTRALIAN RECORDS:** NSW, 33°52'S 151°14'E, in a garden, Elizabeth Bay, Sydney. Coll./pres: J.J. Fletcher (November 1924), AM W 1382; also recorded from Tasmania (Blakemore 2000).

**Description (after Dugès 1837; Pickford 1937; Gates 1972; Bouché 1972; Sims and Gerard 1999)**

Length 10–55 mm. Width 1–3 mm. 73–91 segments. Unpigmented; luminescent in life. Prostomium epilobous, open, 1/3–2/3. Setae 4 pairs per segment;  $aa = bc$ ;  $dd > aa > cd > ab$ ; postclitellar  $aa: ab: bc: cd: dd = 2.0: 1.0: 1.8: 1.6: 3.6$ ;  $dd = 0.25$  u (said by Gates 1972 to be 0.5 u). Dorsal pores absent. Clitellum annular, XIII,  $1/n$ XIII, XIV– $1/n$ XVI, XVI,  $1/n$ XVII, XVII, sometimes incomplete ventrally on the first and last segments. Nephropores of II–IV in  $d$  lines; then in  $c$  or below this to as far as  $b$  lines. Female pores at or slightly median to  $a$  lines, about half way between 13/14 and equator of XIV. Male and prostatic pores both paired on XVII, in  $ab$ ; the male pores near setal lines  $a$  and the prostatic pores near setal lines  $b$ ; penial setae present between the male and prostatic pores (Sims and Gerard 1999); however, Pickford (1937), Gates (1972) and Bouché (1972) state that the male pores lie between the penial ('copulatory') setae of  $ab$ . Prostatic pores, common opening of a prostate and of its adjacent  $b$  follicle, lateral to male pore (Pickford 1937; Gates 1972); or just above the penial setae (Bouché 1972). Genital markings, circular to shortly elliptical and then transversely placed, unpaired, median or lateral, each with a greyish translucent centre (Gates 1972); variable mamillae are present around each male pore (Bouché 1972). Spermathecal pores a pair, each often on a small tubercle, in 8/9, in  $a$  or  $ab$  lines.

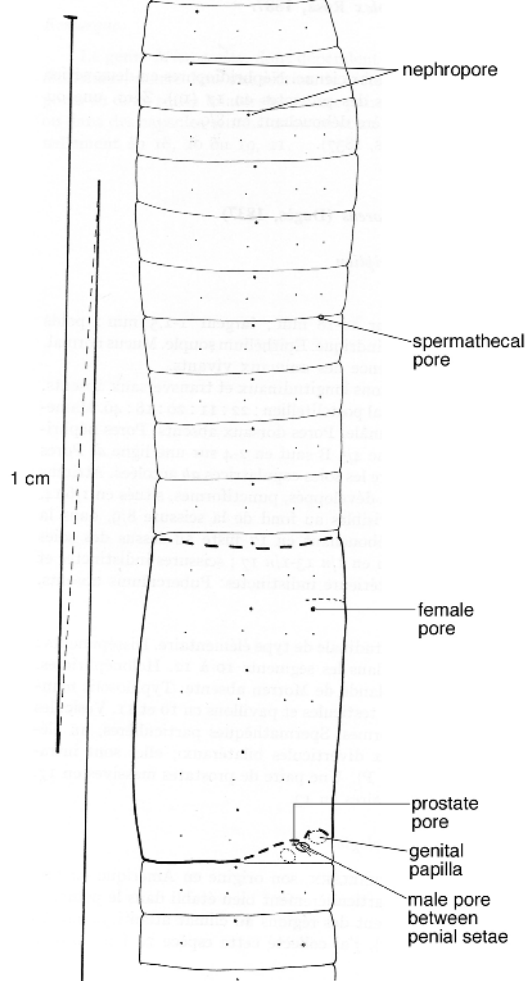
First septum 4/5; 7/8–10/11 or 12/13–13/14 somewhat thickened. Gizzard absent or rudimentary, in V. Calciferous glands absent. Intestine commencing in XVI; typhlosole absent. Dorsal blood vessel single; hearts in X, XI and XII. Nephridial vesicles small anteriorly at or above  $d$  lines; posteriorly large, ocarina-shaped with pointed end continued medially by a slender cord, laterally with bluntly rounded end, funnel-shaped floor narrowing ventrally to parietes (with well-developed parietal sphincters?), tubular portion of the nephridium joining vesicle dorsally and medially. Holandric, testes and funnels paired

**Figs 146, 147, *Microscolex phosphoreus* (Dugès, 1837).** 146, lateral view of anterior region; 147, diagram of a cuticle preparation from the region of the left male and prostatic pores of a mature specimen from Messina, Sicily, showing the separate openings of the two penisetal sacs and the vas deferens, and the union of the prostate duct with the neck of penisetal sac  $b$ .

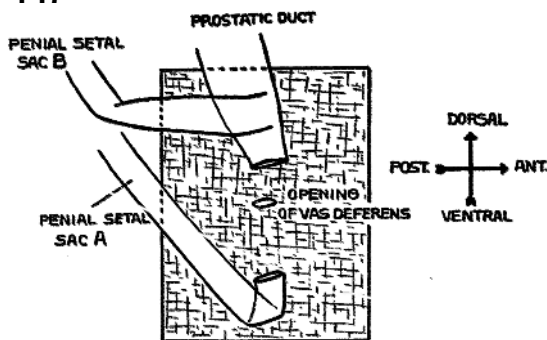
[146, modified after Bouché 1972: 671;

147, from Pickford 1937]

146



147



in X and XII. Seminal vesicles in XI and XII, racemose, reniform. Ovaries, usually with four egg strings, in XIII. Ovisacs small, lobed. Prostates occupying one or two segments, XVII, or XVII and XVIII, the gland thick and tubular, slightly curved or S-shaped; duct moderately long and thin, somewhat coiled or bent. Penial setae of the *a* and *b* bundles alike; long, with slender shaft, gently curved in an S-shape, or slightly if at all curved but distally somewhat more curved and slightly flattened but not broadened, with inconspicuous small broad teeth or serrated scales. Spermathecae 1 pair, in VIII, duct short to nearly as long as the ampulla, with single short, club-shaped medial diverticulum; or (Bouché, Gates) two, equi-sized

or subequal, bilateral diverticula, opening into the basal region of duct, or varying from one to two diverticula (Pickford).

### Remarks

The above account is taken from the sources referred to in the abbreviated synonymy. This species is often parthenogenetic, gametogenesis does not involve polyploidy. It is circummundane but is supposedly indigenous in S South America (see Gates 1972). *Microscolex phosphoreus* differs notably from *M. dubius* in not having a common male and prostatic atrium on each side, in possessing spermathecae and supposedly in its well proven bioluminescence.

*Neodiploptrema* Dyne 1997

*Neodiploptrema* Dyne, 1997: 139–140.

**TYPE SPECIES:** *Neodiploptrema tumida* Dyne, 1997

*Neodiploptrema*; Jamieson 1997: 244.

**Diagnosis**

Setae 8 per segment. Prostates 2 pairs, tubular, their pores on XVII and XIX, or, exceptionally, a single pair, on XVII. Male pores in XVIII, or, rarely (microscolecin condition), closely associated with a single pair of prostatic pores on XVII. Spermathecal pores 2 pairs, in 7/8 and 8/9, or a single pair, in 8/9 only. Gizzard very well developed, in V. Calciferous glands present or absent. Meronephric, avesiculate; anterior tufted nephridia present. Holandric, or, less commonly, metandric. Testis-sacs absent. Penial setae invariably present; genital setae usually present, but occasionally lacking.

**DESCRIPTION (after Dyne 1997; Jamieson 1997)**

Small to large terrestrial worms (48–465 mm in length) with 130–500 segments. Body circular in cross-section. Prostomium pro-epilobous to epilobous. Dorsal and median ventral groove absent. Dorsal pores commencing from 8/9 to 11/12. Setae closely paired, commencing on II; ventral intersetal distance (*aa*) not greatly different from that (*bc*) separating the lateral setae; ventral and dorsal setal couples of similar width; dorsal median intersetal distance (*dd*) > 40 % of the body circumference in the forebody. Setae of XVIII, or the ventral setal couples lacking; ventral setal couples of XVII and XIX modified as enlarged penial setae, or, rarely, only those of XVII thus modified (in *N. deminutionis*); ventral setal couples of IX modified as enlarged genital setae, or undifferentiated. Nephropores numerous and usually inconspicuous. Clitellum saddle-shaped, or annular, occupying XIII to XVI–XVIII. Two pairs of prostatic pores, equatorial on XVII and XIX, coincident with the penial seta orifices, or (*D. deminutionis*) a single pair of combined male and prostatic pores on XVII. Male pores a pair of openings in seminal grooves (the latter well developed or very faint), presetally, or far anteriorly, in XVIII (rarely in the microscolecin arrangement). Accessory genital markings present in some of the segments VIII–XXXII, usually intersegmental, rarely absent. Female pores paired, presetal, median to lateral of *ab*, in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or near *ab*, exceptionally in 8/9 only.

Some pre-clitellar septa thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, some of the commissurals posteriad

of and including X latero-oesophageal, dorsal commissural vessels commencing in VI–VII; supra-oesophageal vessel limited to the oesophagus; subneural vessel absent. Gizzard large, often strongly muscular, in V. Calciferous glands absent, or developed as sessile pouches in the posterior oesophageal region. Intestine commencing in XVII–XX, a dorsal typhlosole well developed. Nephridia in the midbody astomate or stomate, exonephric; caudally nephridial bodies enlarged, each or only the median nephridium with a pre-septal funnel; extensive tufting present in all or some of segments III–V. Enteronephry not developed but longitudinal caudal ureters sometimes present. Holandric, sperm funnels free in X and XI, or metandric, the funnels in X absent. Seminal vesicles present in IX and XII, or in XI and XII, or XII only. Prostate glands tortuous tubes usually restricted to their segment of origin; posterior pair usually conspicuously smaller than the anterior set, or (*D. deminutionis*) totally lacking; prostatic ducts moderately long to long, muscularised. Penial seta follicles usually with copulatory musculature. Ovaries (conjoined oocytic strings) and medium-sized oviducal funnels present in XIII; ovisacs present. Spermathecae subequal, or the posterior pair slightly the larger; the single diverticulum invariably sessile, and provided with numerous intramural sperm chambers.

**Distribution**

Cape York Peninsula, in monsoonal semi-deciduous vine-forests in the Lockerbie, Iron Range and Weipa areas, and the Altanmoui Range; islands of the Torres Strait. One species from near the Tropic of Capricorn in the vicinity of Rockhampton.

The three species, *Neodiploptrema altanmoui*, *N. mcdonaldi*, *N. paripunctata*, and the uncertainly placed *N. ambrosensis*, represented a significant extension of the known range of the genus to the east of the northern continuation of the Great Dividing Range. When first erected, the genus was known only from monsoonal semi-deciduous vine forests in the Lockerbie, Iron Range and Weipa areas, and Thursday Island (Dyne 1997), that is the western and northern flowing catchments at the tip of the Cape York Peninsula. In the more recently demonstrated localities the genus is sympatric with *Diploptrema*.

**Remarks**

The morphological similarities of *Neodiploptrema* to the Australian acanthodriline genus *Diploptrema* are so close that origin of *Neodiploptrema* species



from the latter seemed indisputable (Dyne 1997). Relationship of *Neodiploptrema* to *Diploptrema* has been confirmed from analysis of 28S + mitochondrial 12S +16S rDNA sequences (see Jamieson 2000; Jamieson *et al.* 2002) (Fig. 3). Whether *Neodiploptrema* has a sister group relationship to *Diploptrema* or has originated more than once within that genus, i.e. is paraphyletic, is equivocal (see below). If the latter, *Diploptrema* would be monophyletic only if *Neodiploptrema* were subsumed in it.

Synonymy of *Neodiploptrema* in the New Zealand *Octochaetus* is not here supported as the meronephridia of that genus are radically different and morphological and geographical evidence is strong for local, and probable repeated, derivation in Queensland of the neodiploptreman nephridial condition from the holonephric *Diploptrema*. Such multiple derivation of meronephry from holonephry is well exemplified by New Zealand genera (see Rejection of Octochaetidae *sensu* Gates, above).

As discussed above, molecular analysis showed that *Neodiploptrema* is unequivocally a member of the Acanthodrilinae (*sensu* Jamieson 1971a)

whereas the classification of Gates (1959, 1972) would have demanded its separation in a polyphyletic Octochaetidae defined by tubular prostates and meronephridia (represented in the molecular analysis by *Dichogaster* and *Neodiploptrema*). Furthermore, the Acanthodrilidae when defined as in Gates (1959, 1972) by tubular prostates and holonephridia (represented in the analysis by *Fletcherodrilus*, *Terrisswalkerius*, *Diporochaeta*, an argilophilin, *Pontodrilus* and *Diploptrema*) was shown to be highly polyphyletic.

While suppression of Gates' Octochaetidae, and close affinity of meronephric and holonephric forms (e.g. *Neodiploptrema* and *Diploptrema*) is incontrovertible, it is probable that the meronephric condition of species attributed to *Neodiploptrema* has originated more than once from the holonephric *Diploptrema* condition (see Remarks under *N. ambrosensis* and *N. mcdonaldii*), thus rendering *Diploptrema* paraphyletic. In the molecular analysis the two genera were sister-groups but a larger contingent of species is needed to confirm this. The very large ratio of *dd: u* is a further link between the two genera.

## CHECKLIST OF AUSTRALIAN SPECIES OF *NEODIPLOPTREMA*

*Neodiploptrema altanmoui* Jamieson, 1997  
*Neodiploptrema ambrosensis* (Blakemore, 1997)  
 (*Diploptrema*?). New combination  
*Neodiploptrema deminutionis* Dyne, 1997  
*Neodiploptrema exigua* Dyne, 1997  
*Neodiploptrema lacisbrontoi* Dyne, 1997

*Neodiploptrema mcdonaldii* Jamieson, 1997  
*Neodiploptrema occidentalis* Dyne, 1997  
*Neodiploptrema paripunctata* Jamieson, 1997  
*Neodiploptrema raveni* Dyne, 1997  
*Neodiploptrema tumida* Dyne, 1997  
*Neodiploptrema varionephrica* Dyne, 1997

## KEY TO AUSTRALIAN SPECIES OF *NEODIPLOPTREMA*

- 1 a. Male apparatus acanthodrilin: 2 pairs of prostatic pores in XVII and XIX, male pores separate, on XVIII . . . . . 2
- b. Male apparatus microscolecin: a single pair of prostatic pores associated with the male pores on XVII . . . . . *N. deminutionis*
- 2(1a) a. Male organs metandric . . . . . 3
- b. Male organs holandric (though there may be some reduction in X) . . . . . 4
- 3(2a) a. Paired papillae on X, XI and XII, with apical genital setae . . *N. ambrosensis*
- b. Paired papillae on VIII. Genital setae absent? . . . . . *N. occidentalis*
- 4(2b) a. Seminal vesicles in IX and XII . . . . . 5
- b. Seminal vesicles in XI and XII . . . . . 8
- 5(4a) a. Penial setae with trifid tips . . . . . *N. varionephrica*
- b. Tips of penial setae not divided . . . . . 6

- 6(5b) a. Spermathecal diverticulum sacciform ..... *N. exigua*  
 b. Spermathecal diverticulum multiloculate ..... 7
- 7(6b) a. Strong denticulation of the penial setae present, paired, apposed genital markings posteriorly in 15/16 absent ..... *N. altanmoui*  
 b. Strong denticulation of the penial setae absent, paired, apposed genital markings posteriorly in 15/16 present ..... *N. paripunctata*
- 8(4b) a. Spermathecal diverticulum mammillated, exceeding the length of the ampulla. Penial setae sinuous and hair-like ..... *N. mcdonaldi*  
 b. Spermathecal diverticulum not mammillated. Penial setae not sinuous and hair-like ..... 9
- 9(8b) a. Genital setae well developed, in IX. Prominent genital markings present in the region of XVIII–XXI. .... *N. tumida*  
 b. Genital setae absent or rudimentary. Genital markings absent from the region of XVIII–XXI ..... 10
- 10(9b) a. Moderately large worms (150–200 mm); ventral setal couples of XVIII lacking, oesophagus with conspicuous outpouchings in XIV–XV ..... *N. lacisbronti*  
 b. Very large worms (350 mm); ventral setal couples of XVIII present; oesophageal pouching absent. .... *N. raveni*

***Neodiploptrema altanmoui* Jamieson, 1997**

(Figs 148–152)

*Neodiploptrema altanmoui* Jamieson, 1997: 244–249, fig. 12–16, 39.

**TYPE-LOCALITY:** Qld, 14°33.51'S 144°38.14'E, Altanmoui Section, Cape Melville National Park, alt. 560–570 m, vine forest on sandstone escarpment, under logs and rocks on forest floor. Coll. K. McDonald, P.J. Lethbridge, 8 Apr 1995.

**HOLOTYPE:** QM G211986.

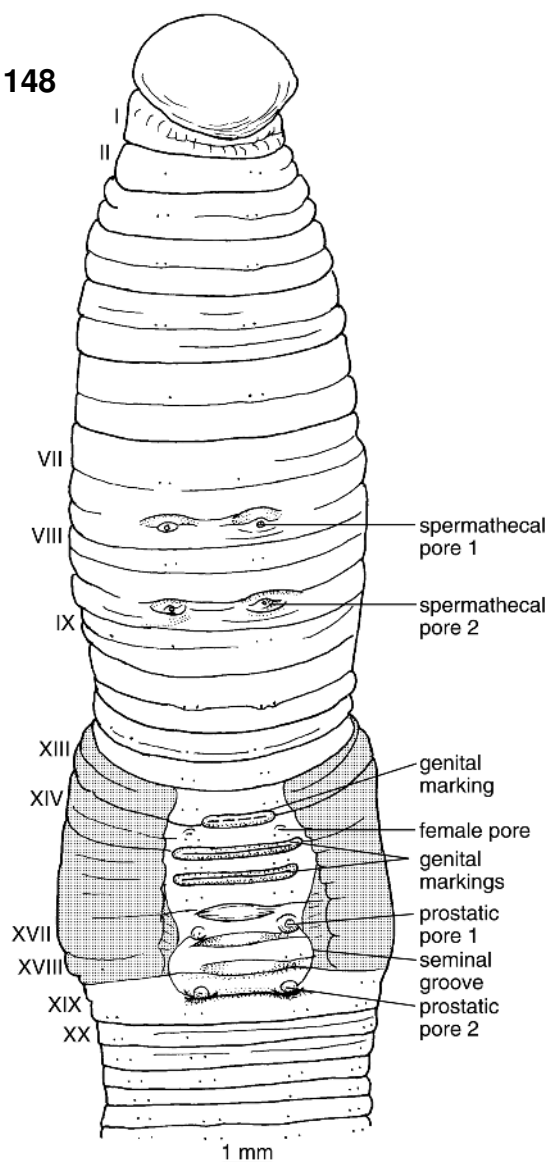
**PARATYPES:** P1 and 2 QM G212023. Same data, in mesophyll vine forest, under rock, Paratype 3 QM G211987.

**Description (after Jamieson 1997)**

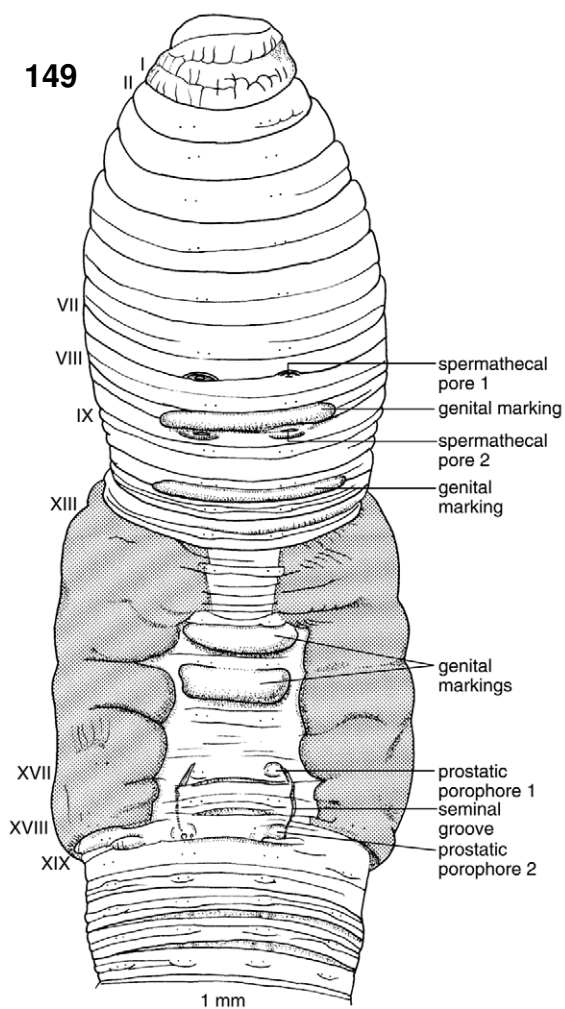
Length 140 mm. Width (midclitellar) 7.6 mm. Segments 258. Circular in cross-section, pigmentless in alcohol. Prostomium wide and prolobous but a suggestion of a narrow continuation onto the much fissured peristomium, a middorsal groove being wider than the others. First dorsal pore 12/13. Setae 8 per segment, in regular longitudinal rows throughout; ventral seta couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; no genital setae; in XII, *aa: ab: bc: cd: dd* = 6.3: 1.0: 7.1: 1.0: 48.3; or 8.7: 1.4: 9.8: 1.4: 66.4%. Nephropores sporadically visible as a transverse series of minute ovals anteriorly in their segments.

Clitellum saddle-shaped, protuberant, over XIII–XVIII; ventral margins well above *b* lines. Prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices, in *ab*, on small subcircular porophores; seminal grooves, joining the prostatic porophores of a side, forming parentheses with their midpoint, and presumably the male pores, lateral of *b* lines at the equator of XVIII, the grooves deeply incised or faint (owing to maceration?); the anterior prostatic pores 2.3 mm, ca 0.1 body circumference apart. Genital markings indefinite in the macerated holotype, whitish somewhat keratinised-looking transverse unpaired midventral ridges in intersegments 13/14, 14/15 and 15/16 (the most pronounced), XX and XXI, including the ventral setal couples which when most clearly defined consist of a narrow ventral band or pad posterior in each of VIII and X and extending well laterally of *b* lines, with their anterior borders at but not including the setal arc; that in VIII posteriorly abuts closely on the spermathecal pores of 8/9; other markings two much larger but transversely less extensive pads one at each of intersegments 14/15 and 15/16 extending shortly lateral of *b* lines, each abutting the ventral setal couples of the previous segment but posteriorly not reaching the following setal arc. Female pores minute transverse slits, each with a crescentic anterior border, immediately anterior to the ventral setal couples, almost in *b* lines. Spermathecal pores 2 pairs, in 7/8 and 8/9,

148



149

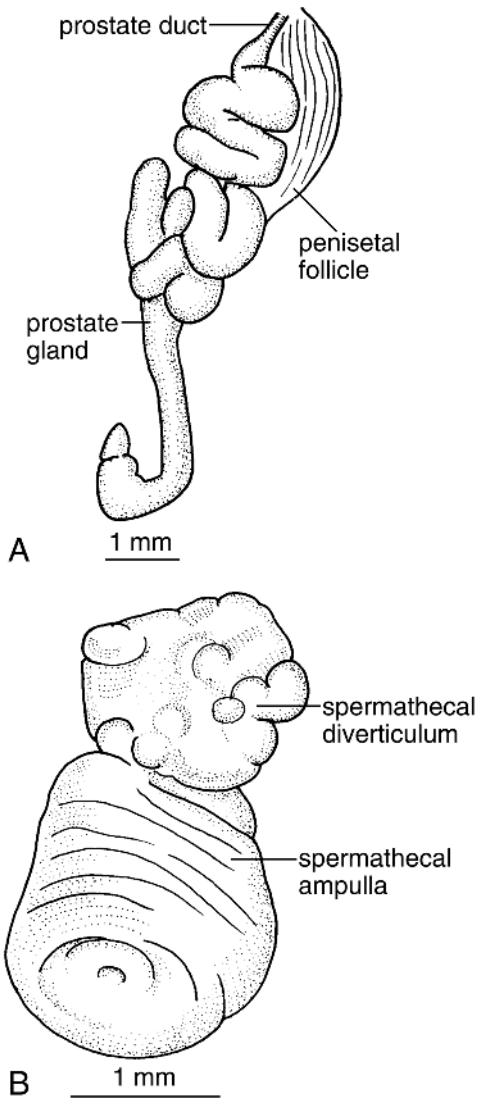


**Figs 148, 149, *Neodiploptrema altanm7oui* Jamieson, 1997. 148, genital field of Holotype; 149, genital field of Paratype 3.** [From Jamieson 1997]

in *ab*, definite pores filled with coagulum and with anterior and/or posterior crescentic lips; those of each pair conjoined by a narrow band medially.

Septa 5/6–10/11, especially 8/9 and 9/10, strongly thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; those in X–XIII latero-oesophageal, with well-developed connectives to the supra-oesophageal vessel and

much thinner connectives to the dorsal vessel; commissurals in IX and anteriorly slender with dorsal connectives only. Gizzard large, stoutly cylindrical, firm and muscular in V. Oesophagus lacking calciferous glands; transition from oesophagus to intestine indefinite in terms of appearance of the gut wall and presence of fine, silty contents, but not widening until XX; a low, narrow dorsal typhlosole commencing behind the



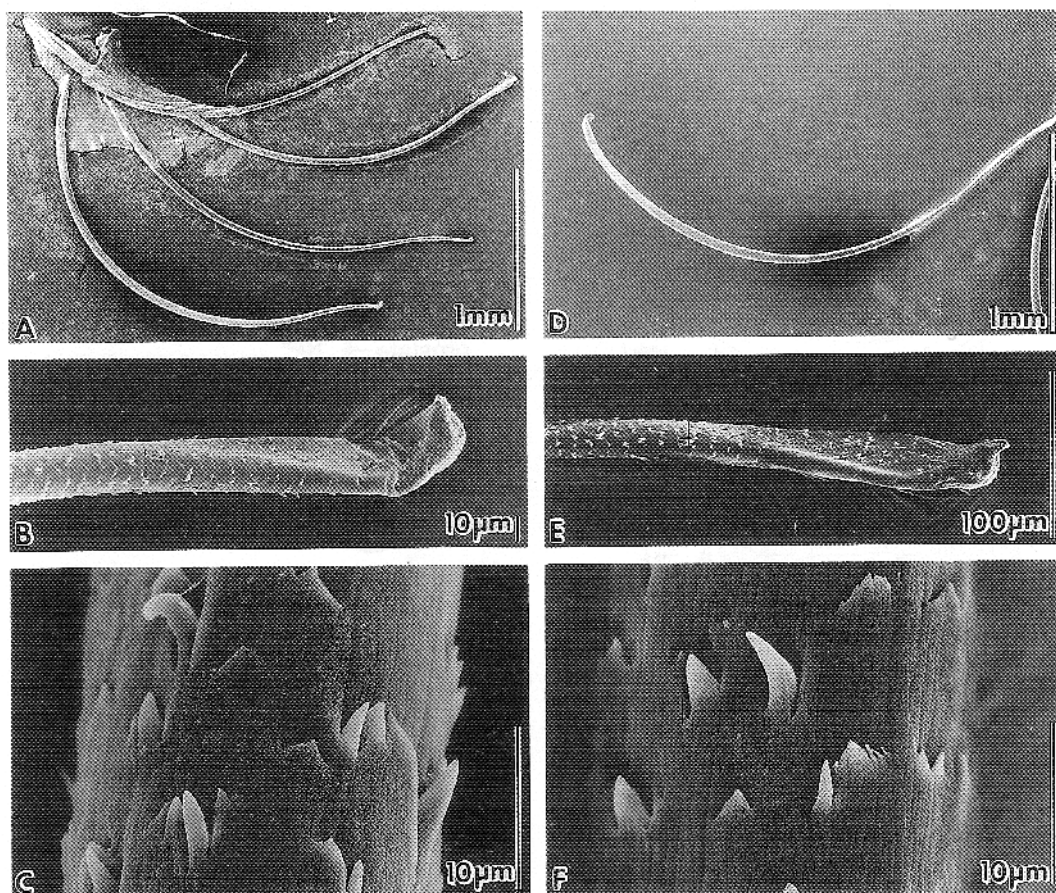
**Fig. 150.** *eodiploptrema altanmoui* Jamieson, 1997. Paratype 1: **A**, right prostate of XIX; **B**, right spermatheca of IX. [From Jamieson 1997]

prostates. Meronephric throughout, nephridia commencing in II; very conspicuous, profusely divided tufts present in III and IV, very large and restricted to IV, a thick duct of each tuft running anteriorly, to the wall of the buccal cavity. In the midbody, shortly behind the prostates, approximately 8 astomate micromeronephridia on each side and a median, not especially enlarged but more convoluted, meronephridium for which a preseptal funnel was demonstrated sporadically. Caudally, the medianmost nephridium is greatly

enlarged relative to those lying more laterally and has a conspicuous preseptal funnel. Holandric; sperm masses, and iridescent funnels in X and XI. Racemose seminal vesicles in IX and XII, those in XII the larger and visible dorsally. Bushy ovaries with few oocytes, in XIII or large, undulating laminae with many oocytes. Prostate glands two pairs of simple, much convoluted tubular organs; both pairs extending back into XXV; the anterior pair somewhat longer than the posterior pair but both pairs well developed; or the anterior pair in XVII and XVIII, the posterior pair in XIX and XX; each with a short slender, slightly muscular duct; or the glands restricted to segments XVII and XIX. Penial setae with two posteriorly joined muscular follicles on each side, each containing two setae, presumably corresponding to *a* and *b* follicles, at each prostate duct; length of a well-developed seta (measured in a straight line from base to tip) = 1.9 mm. The setae bowed through varying degrees, maximally about 90°; the ectal region of the shaft ornamented with circumferential rows of single- or multiple-pointed ectally directed teeth; the tooth rows closely spaced along the seta, approximately 10 µm apart; cross section of the seta circular excepting at the tip which forms an elongate spatula, only slightly concave, with thickened margins, and a knoblike, pointed tip; scattered teeth continuing into the spatulate region; the latter sometimes bent 'dorsoventrally', possibly because of compression during copulation. No notable difference in form observed between setae of XVII and XIX; sometimes with more protuberant thorn-like scales. Spermathecae 2 pairs, in VIII and IX, each organ consisting of a rounded diverticulum sessile on the body wall and obscuring beneath it all but a small ental region of the wide duct and a large saclike ampulla which in the holotype has a series of encircling annuli or pliae; the margins of the diverticulum irregularly and indistinctly lobed owing to many internal sperm chambers; in IX, length right spermatheca = 3.3 mm; length ampulla 2.0 mm; ratio length spermatheca: length duct (with superior diverticulum) = 2.5.

### Remarks

The specimens of *N. altanmoui* were located in moist mesophyll vine forest on the Jurassic Dalrymple sandstone and moist soil where the sandstone escarpment boundary met the Permian Altanmoui granites. It occurs at the headwaters of Wakooka Creek, an eastwards flowing coastal stream arising in the Altanmoui Range. The feather palm forest along drainage lines was dominated by *Archontophoenix* sp. and at an altitude of 540 metres is the highest of this



**Fig. 151.** *Neodiploptrema altanmoui* Jamieson, 1997, Holotype, scanning electron micrographs: **A**, right penial seta of XVII; **B**, ectal region of penial seta; **C**, detail of sculpturing of same; **D**, penial seta of XIX; **E**, ectal region of a penial seta of XIX. [From Jamieson 1997]

vegetation type in the Laura basin (Cooktown to Princess Charlotte Bay) by a large margin (see Jamieson 1997).

*Neodiploptrema altanmoui* resembles the sympatric *N. paripunctata* and the allopatric *N. exigua* Dyne, from Lockerbie East, and *N. varioneprica*, from Lake Bronto. These four species differ from all other known species in the genus in having seminal vesicles in segments IX (in addition to those in XII).

It differs from *N. exigua* in the lobed multiloculate spermathecal diverticulum whereas the latter species has a sacciform, blunt diverticulum and in the more anterior origin of the intestine. *N. altanmoui* resembles *N. paripunctata* in the form of the spermathecae, with a rosette-like arrangement of loculi of the spermathecal

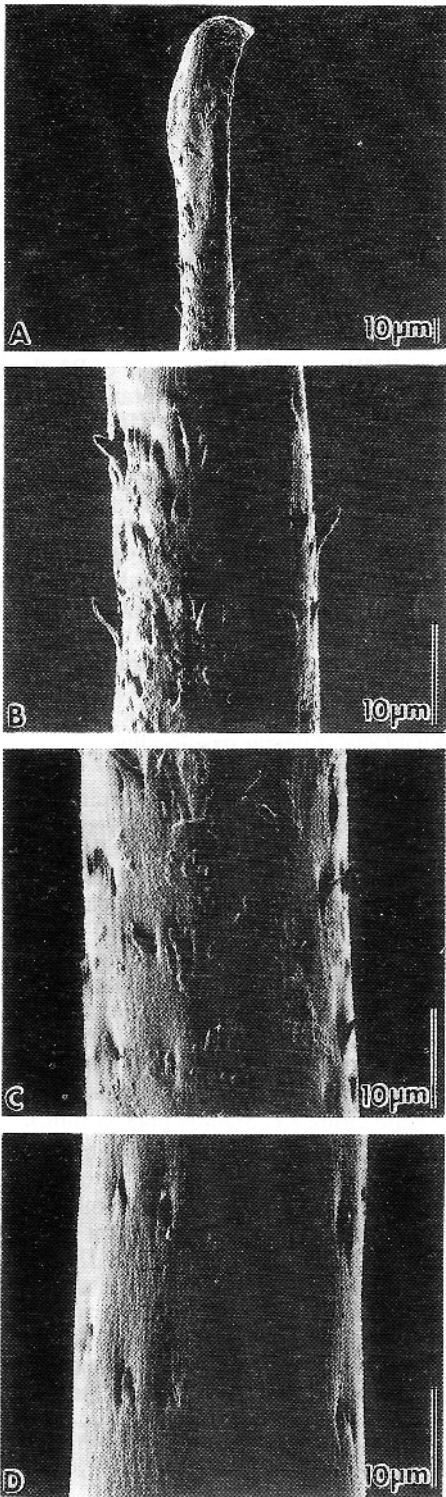
diverticulum on the short spermathecal duct. Differences from the latter species are numerous and include the distinctive setal ratios, the strong denticulation of the penial setae, and the absence of the paired, apposed genital markings posteriorly in XV. *N. varioneprica* is readily distinguished from it by the trifid tips of the penial setae.

***Neodiploptrema ambrosensis*  
(Blakemore, 1997)**

New combination

***Diploptrema* (?) *ambrosensis*** Blakemore, 1997: 1790–1792, fig. 1.

**TYPE LOCALITY:** Qld, 23°48'S 150°55'E, from Hut Creek near confluence with Four Mile Creek, SW of Ambrose near Rockhampton.



**PARATYPE LOCALITY:** Qld, junction Gentle Anne to Old Langmorn School Rd.

**HOLOTYPE:** ANIC RB.94.4.1.

**PARATYPES:** ANIC RB.94.4.2–4.

**Description (after Blakemore 1997)**

Anterior region bulbous with distinct waist in clitellar region. Length 100–250 mm. Width 9 mm. Segments ca 202–482; secondary annulation obscures true furrows (external segmentation detected largely by setae). Colour pink in life with dorsal blood vessel visible; unpigmented white in formalin; clitellum faintly yellow. Prostomium pro-epilobous, deeply furrowed as are first two or three segments. First dorsal pore 11/12(?), pores continuous on clitellum. Setae minute, not detectable on anterior to about X, thereafter seen as closely paired couples; *ab* retained on XVIII; approximate setal ratios on XII 30: 1:20: 1: 70: 0.5; genital setae (ventral setal couples) of X, XI and XII on prominent mounds; penial setae-tips protrude on XVII and XIX, ca 5 mm long and curved with scalloped tips. Nephropores not found (but small anterior pores near *c* lines seen in one specimen). Clitellum XII–XVII, XVIII, XIX visible dorsally only as yellow tint and constriction. Male pores: not found, faint seminal grooves visible between laterally displaced *b* penial setae of XVII and XIX. Genital markings: genital setae apical on paired papillae of X, XI and XII; elongate ventral pads displace the equators and reach to the succeeding intersegmental furrow in XIII and XIV or XIV–XVI or XIII–XV; a smaller elongate pad in midventral setal gap in 19/20 in holotype. Female pores minute (large postsetal mound in XIV bears two small pores that may actually be 'amphimixis scars?'). Spermathecal pores 2 pairs, ellipsoid in 7/8 and 8/9 lateral of extrapolation of ventral setal series.

Septa 4/5 thin but distended by tufted nephridia in IV; 5/6 thin to base of gizzard; 6/7–10/11 thickening slightly; 9/10–11/12 moderately thick, then thinning to become membranous by 14/15; 5/6–8/9 displaced by gizzard, 10/11 and 11/12 adherent. Dorsal blood vessel single from VI. Hearts in X–XIII. Gizzard strongly muscular tapering cone in V with anterior flange. Calciferous glands absent but oesophageal dilations in XII–XIII or VIII–X. Intestinal origin XV; thick, but low, typhlosole commencing after about XXV–XXVIII; acaecate. Gut contents fine,

**Fig. 152, *Neodiplotrema altanmoui*** Jamieson, 1997, Paratype 3, scanning electron micrographs of right anterior penial seta: **A**, tip of seta; **B–D**, progressively more posterior regions of the anterior ornamentation.

[From Jamieson 1997]

flocculated, reddish soil. Nephridia: pharyngeal tufts filling IV (and III?); smaller tufts paired from V but doubling to form two pairs around X–XII; from clitellar region four to six discrete tubules forming equatorial bands on the body wall on each side that are laterally connected by mesentery [funnels not mentioned]. Metandric, testes iridescent in XI only; small, paired racemose seminal vesicles in XII. Ovaries in XIII, long palmate egg-strings. Prostates 2 pairs, tortuous, tubular, in XVII and XIX, each with a short muscular duct and overlain by enormous penial setal sheaths; anterior pair substantially larger than posterior pair. Spermathecae 2 pairs, in VIII and IX; posterior pair slightly larger; duct long, ampulla spherical, diverticulum sessile, buckle-like and equisized with ampulla.

### Remarks

Although this species conforms to *Neodiploptrema* in being meronephric, Blakemore (1997) considered that the closest relationship might be with three *Diploptrema* species from Rockhampton: *D. schmardae*, *D. daemeli* and *D. queenslandica*. He states that by being metandric and having genital setae in X–XII (rather than some of VII–X), it is differentiated from all known species of *Diploptrema*. However, the holonephric *Diploptrema acropetra* Jamieson, 1997, is also metandric, and has genital setae in X and XI, and is possibly a close relative. In the location of genital setae *N. ambrosensis* differs from the other species of *Neodiploptrema*. It is possible that the meronephric condition has developed in this species independently of the other, more northerly species of *Neodiploptrema*.

### *Neodiploptrema deminutionis*

Dyne, 1997

(Figs 153, 154)

*Neodiploptrema deminutionis* Dyne, 1997: 141–142, fig. 2, 11B

**TYPE LOCALITY:** QLD, 1046'S 14234'E, on the eastern side of Lake Bronto, Cape York Peninsula, in open eucalypt forest in dark sandy soil. Coll. R. Raven, 4 Feb 1975.

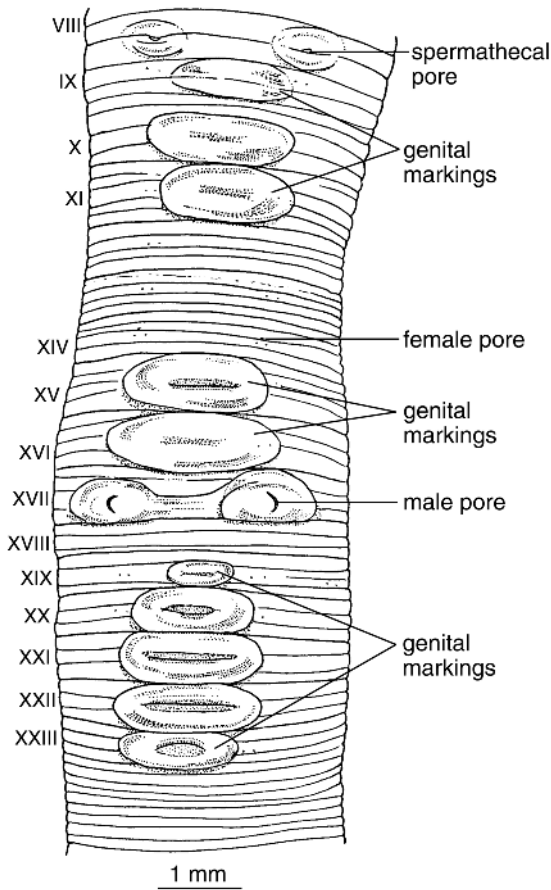
**HOLOTYPE and 8 PARATYPES:** ANIC GD.95.31.1

### Description (after Dyne 1997)

Length 140 mm. Width 2.7–2.9 mm. Segments 311. Uniformly circular in cross-section throughout; pigmentless buff in alcohol. Prostomium prololous, first dorsal pore pre-9/10. Setae in regular longitudinal rows, closely paired throughout; ventral setal couples of XVIII normal, those of XVII modified as enlarged penial setae; genital setae lacking. Nephropores inconspicuous.

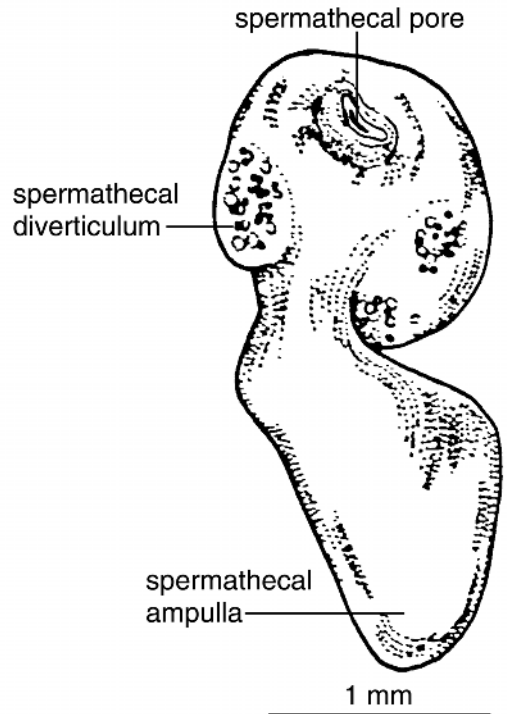
Clitellum not developed in any of the specimens available for study. Combined male and prostatic pores in distinct longitudinal slits on raised papillae, in XVII, coincident with the openings of the penial setae. Serial sectioning reveals that the vasa deferentia and prostatic ducts do not actually fuse, but open contiguously at the common pore. Female pores visible as tiny, transverse slits presetally, in *ab*, usually with swollen rims. Accessory markings a series of unpaired, median, intrasegmental pads: a small ellipsoidal pad in X, or IX also, extending across *aa*; a similarly sized swelling in XI or absent (all the above markings have shallow, transversely concave centres); a pad is located in XV, transverse width = *aa* with a larger marking in XVI, across *bb* (most specimens); another series of similar markings present in the post-genital region: a diminutive tumescence in some or all of XIX, XX (a much larger, across *aa*), or similarly in XXI, and a further small marking usually present in XXII.

Septa 10/11, 11/12 slightly thickened, 6/7–9/10 moderately strongly muscularised, 5/6 slightly thickened, encapsulating the gizzard. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel present VII–XIX, adherent to the roof of the oesophagus, and receiving vessels from oesophageal blood plexi, particularly in XII–XIV. Last hearts in XIII, those in X–XIII receiving thin connectives from the dorsal vessel, and more strongly developed ones from the supra-oesophageal vessels; commissurals XII and XIII much larger than the remainder, which decrease in size anteriorly, those anterior to X dorsoventral only. Gizzard large, shiny, but compressible in V, with a slight dorso-ventral compression. Oesophagus rather narrow, constricted intersegmentally, with conspicuous rugae on its inner walls, and extending from VI to XVI. Intestinal origin, commencing with abrupt expansion, in XVII, or XVI?; somewhat paler and apparently less muscular anterior of XXIV. An extremely well-developed rugose dorsal typhlosole commences in XXII. Meronephric throughout; considerable tufting in IV, with many highly coiled loops, and composite ducts sent to the pharynx; the remainder of the nephridia comprise very numerous astomate exonephric loops scattered on the body wall and septa, larger and more numerous in the oesophageal region. Caudally, the bodies again enlarged, each apparently with a distinct preseptal nephrostome; no enteronephry demonstrable. Holandric; 2 pairs of small, iridescent funnels in X and XI, attached ventrally to septa 10/11 and 11/12; large, subequal, racemose seminal vesicles in XI and XII, anteriorly attached to septa 11/12 and 12/13,



**Fig. 153.** *Neodiploptrema deminutionis* Dyne, 1997, genital field of Holotype. [After Dyne 1997]

composed of large, conspicuous loculi. Vasa deferentia obvious as closely paired, slightly iridescent tubes tortuously adherent to the body wall on either side of the oesophagus; the paired ducts become fused in the parietes, in XVII. Prostate glands a pair of flattened, loosely coiled tubular organs lying in segment XVII, with long, muscular (shiny) ducts opening to the exterior slightly ventral of the vasa deferentia. Penial seta follicles large, gently curving, copulatory musculature well developed, inserted near the mid-dorsal line; the setae with a gradual bend, the shaft divided into an ectal region devoid of ornamentation, with an intervening section bearing scattered solitary or clustered thorn-like spines with rather broad bases, and narrowing to a fine point (these stand out at an angle to the shaft); the entire ectal portion is approximately equal to the ornamented section, and these together constitute



**Fig. 154.** *Neodiploptrema deminutionis* Dyne, 1997, left spermatheca of IX, Holotype. [After Dyne 1997]

about half of the total length of the seta. Length mature seta 2.35 mm; midshaft diameter 25.5  $\mu$ m (mean of 3). Genital seta follicles absent. Ovaries, consisting of thin sheaves of small oocytes, together with medium-sized diaphanous funnels, are present XIII, ovisacs absent. Spermathecae a single pair, divided into a stalked, sacciform ampulla, and a broadly U-shaped diverticulum which is completely sessile, and occupies the entire dorsal aspect of the short duct; the walls of the diverticulum are studded with numerous iridescent intramural sperm chambers; the ampullal 'stem' is swollen at its junction with the diverticulum. Length of right spermatheca of IX 2.6 mm (apex of ampulla to pore).

#### Remarks

*N. deminutionis* is the only known microscolecin *Neodiploptrema* species and has a distinctive array of genital markings. The latter are atypical of the genus in being intrasegmental. *N. deminutionis* is sympatric with *N. lacisbrontois* and *N. varioneprica*, but neither of these species appears to be convincing as an acanthodrilin precursor of this species (Dyne 1997).



***Neodiploptrema exigua* Dyne, 1997**

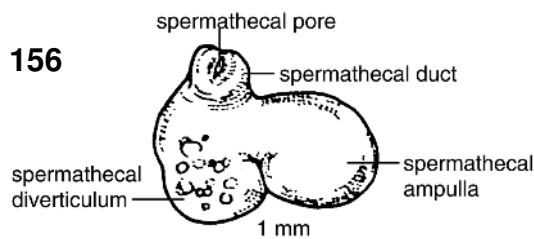
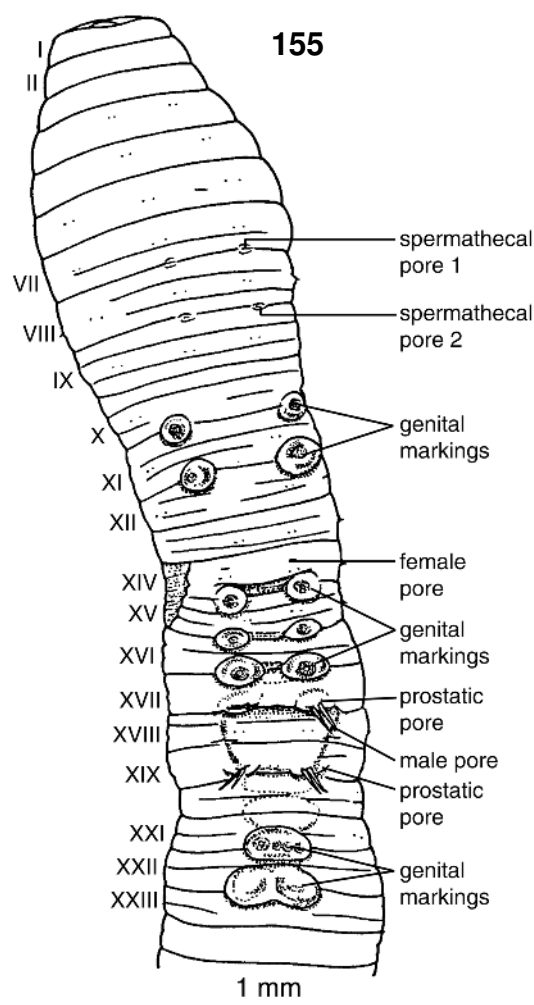
(Figs 155, 156)

***Neodiploptrema exigua* Dyne, 1997**–144, figs 3, 11C.**TYPE LOCALITY:** Qld, 10°48'S 142°28'E, Lockerbie East, soil over rocky substrate, in dense semi-deciduous vine-forest. Coll. R. Raven, 1 Feb 1975.**HOLOTYPE:** QM GH2889**PARATYPE:** QM GH2890**OTHER MATERIAL:** Qld, 10°48'S 142°28'E, Lockerbie East, under logs near 'Mango Tree camp'. Coll. R. Raven, 30 Jan 1975 (3 immature-semi-mature specimens, not designated as types), ANIC GD.95.9.3.**Description (after Dyne 1997)**

Length 48–64 mm. Width (midclitellar) 1.7 mm. Segments 136–149. Uniformly circular in cross-section, pigmentless buff in alcohol. Prostomium probolous; first dorsal pore 11/12 (imperforate). Setae 8 per segment, commencing in II; ventral setal couples of XVIII present; those in XVII and XIX modified as enlarged penial setae; genital setae lacking. Nephropores not visible externally. Clitellum very faint, barely distinguishable. Male pores located presetally, in definite seminal grooves, on XVIII, lateral of *b* lines. Prostatic porophores 2 pairs, in XVII and XIX, each on a distinct papilla, and intimately associated with (usually) protuberant penial setae. The slightly convex male field is delimited laterally by the seminal grooves (joining the prostatic pores of a side), with the prostatic porophores defining its corners. Female pores small slits presetal in XIV, in *ab*. Accessory markings 2 pairs of rounded tumescences with oculate centres present intersegmentally, in 10/11 and 11/12; a further series of three more closely paired markings (of similar shape) present in 14/15 and 16/17, slightly lateral of *b* lines; the markings in 14/15 are separated by a distinct depression, the remainder to a much lesser extent; a diffuse and indistinct pad extending from the posterior edge of the male field to the anterior portion of segment XXI is seen to be of width *bb*; 2 further unpaired median markings are located in 21/22 and 22/23, the former the smaller, with a multi-oculate central area, the marking in 22/23 longer, almost paired, with central depressions. Spermathecal pores 2 pairs of simple depressions, in 7/8 and 8/9, in *ab*.

Septa 5/6 delicate, 6/7–7/8 slightly thickened, 8/9–12/13 moderately muscularised, 13/14 slightly affected, remainder diaphanous. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X–XIII considerably larger

than the remainder, with connectives from both the dorsal and supra-oesophageal vessels; the latter vessel moderately developed, its limits not determinable. Gizzard large, though compressible, in V; oesophagus narrow, VI–XIX, but with three pairs of obvious pouches in XVI–XVIII, that closely resemble stalked calciferous glands; these are complexly vascularised, and contain conspicuous lamellae; the three pouches on each side of the oesophagus are clearly interconnected, but communication of each of the pouches independently to the oesophagus could not be demonstrated. Intestinal origin XX, a robust, though flattened, dorsal typhlosole is present after XXV. Meronephric; the mid-body segments each containing a pair of large megameronephridia with preseptal nephrostomes, their terminal ducts discharging to a pair of ventral, longitudinal ureters that run the entire length of the body, opening at the anus; the megameronephridia decrease gradually in size posteriad, and disappear abruptly approximately 25 segments from the posterior end; in addition to the above, each intestinal segment contains 3 pairs of small, astomate, exonephric loops, distributed evenly on each side of the nerve-cord, the dorsalmost body just below the mid-dorsal line; these persist (perhaps with some slight trend towards a size increase) to the caudal extremity. A large pair of tufted nephridial bodies is present in V, with a much smaller set in VI. Holandric; large, iridescent spermatid funnels and sperm masses seen in X and XI; 2 pairs of palmate seminal vesicles composed of large, lightly iridescent loculi present in IX and XII, the former somewhat smaller and compressed. Prostate glands 2 pairs of simple tubular structures in XVII and XIX, the anterior pair the larger; the ducts are weakly muscular, and short. Penial seta follicles proportionately large for the species, each follicle with a distinct retractor ligament inserted on the dorso-lateral aspect of the body wall. The setae fairly flat, gently curving, the ectal region with a distinct sinusoidal bend; the ectal  $\frac{1}{4}$ – $\frac{1}{3}$  is ornamented with clusters of 3–4 irregular, jagged teeth. Length mature seta 2.4 mm; midshaft diameter 53.4  $\mu$ m (mean of 3). Ovaries, comprising several strings of medium-sized oocytes, together with small, pleated oviducal funnels, present in XIII; minute rounded structures on the posterior face of septum 13/14 are questionably ovisacs. Spermathecae rather small, each organ consisting of an ovoid ampulla and sacciform, blunt diverticulum (with some iridescence); duct very short. Length right spermatheca of IX 0.6 mm (base of ampulla to pore). Genital seta follicles absent.



**Figs 155, 156, *Neodiploptrema exigua* Dyne, 1997, Holotype. 155, genital field; 156, right spermatheca of IX.**  
[After Dyne 1997]

### Remarks

This small species has undoubted affinities with *N. varionephrica*, both species possessing a remarkable nephridial system which incorporates a

combination of micromeronephridia and megameronephridia, the latter with longitudinal ureters.

Apart from the nephridial modifications, which together with the absence of genital setae, serve to distinguish it from its congeners, *N. exigua* is otherwise unremarkable, there being little to justify the erection of a higher taxonomic category (i.e. a subgenus) to accommodate it and *N. varionephrica* (Dyne, 1997). It may here be added that if *Neodiploptrema*, or at least some species of it, arose within *Diploptrema*, recognition of it would render *Diploptrema* paraphyletic. It remains taxonomically convenient (i.e. informative), nevertheless, to recognise meronephric species as a distinct entity, the genus *Neodiploptrema*. Furthermore, molecular data (Fig. 3), albeit for only one species, *N. altanmoui*, are not unsupportive of recognition of separate generic status for at least this species.

### *Neodiploptrema lacisbrontoi* Dyne, 1997

(Figs 157, 158)

*Neodiploptrema lacisbrontoi* Dyne, 1997: 144–146, figs 4, 11D.

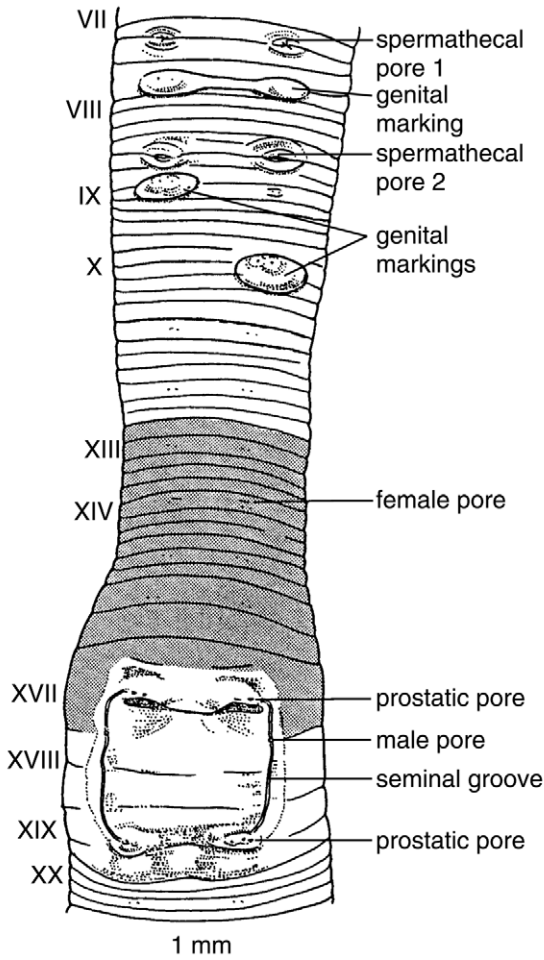
**TYPE LOCALITY:** Qld, 10°46'S 142°34'E, dense rainforest at northern end of Lake Bronto, in openings in forest canopy, black sandy soil, dense leaf and twig litter, some ground cover, 1 m deep. Coll. R. Raven, 4 Feb 1975.

**HOLOTYPE:** QM G211957.

**PARATYPE:** QM G211958 (4 specimens).

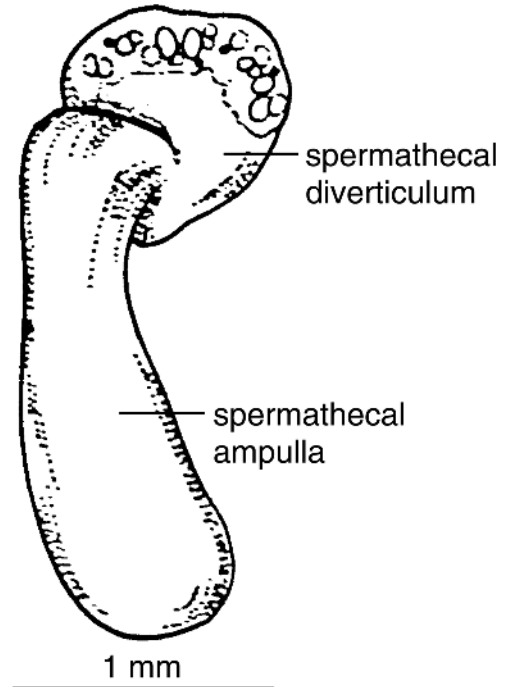
### Description (after Dyne 1997)

Length 140–165+ mm. Width 4.9 mm. Form circular in cross-section throughout, pigmentless buff in alcohol. Prostomium strongly furrowed. First dorsal pore at 9/10. Setae 8 per segment, closely paired, the ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; the ventral setal couple on the left side of X very slightly enlarged, but cannot be regarded as functional genital setae. Nephropores not visible externally. Clitellum annular, fairly strongly developed over XIII–XVII, setae visible. Male pores are situated just posterior to intersegment 17/18, lateral to *b* lines; each surmounts a tiny papilla in a distinctly demarcated seminal groove, which connect the porophores on each side. Prostatic openings, 2 pairs, in XVII and XIX, not on distinct papillae, but rather at the anterior rim of small, circular concavities (more pronounced in the anterior pair), which form the four corners of a roughly square male field. In undissected specimens, this region appears slightly depressed with respect to the remainder of the body surface. Female pores are inconspicuous slits slightly pre-setal in *a* of XIV. Accessory



**Fig. 157.** *Neodiploptrema lacisbrontoï* Dyne, 1997, genital field of Holotype. [After Dyne 1997]

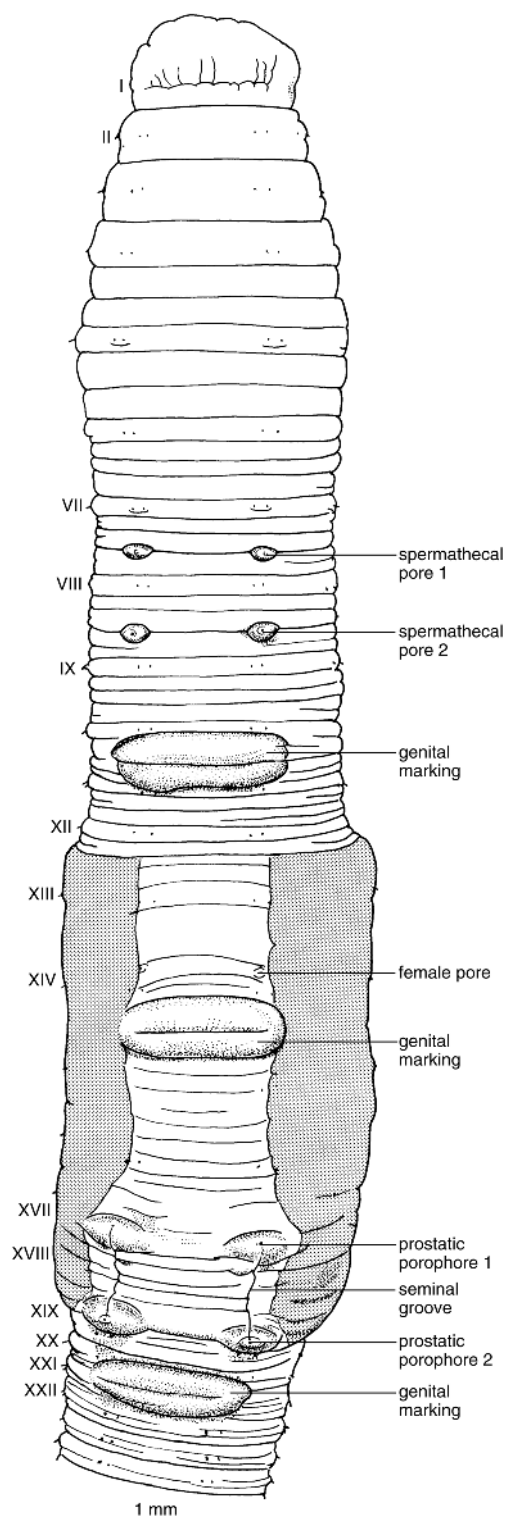
markings a very narrow tumid strip in XXI in aa with central depression; a similar marking in 20/21 without depression; a large tumescent patch in the upper portion of segment XVI, in bb; a papilliform swelling in X, centred on the ventral setal couple, but extending laterally in both directions, as well as anteriad and posteriad (sometimes right side only); a similar marking in IX, centred on ab, but confined within 2 adjacent intrasegmental furrows, or absent; a pair of papilliform swellings in VIII, similarly disposed, but conjoined by a median tumid band, or unilateral only. Spermathecal pores 2 pairs in 7/8, 8/9, each with a conspicuously puckered rim.



**Fig. 158.** *Neodiploptrema lacisbrontoï* Dyne, 1997, right spermatheca of VIII, dorsal view, Holotype. [After Dyne 1997]

Septum 5/6 moderately thickened, septa 10/11, 11/12 strongly so, 6/7–9/10 very much thickened and muscularised. Dorsal blood vessel single, continuous onto the pharynx, where it divides repeatedly. Last hearts in XIII; those in XII and XIII the only large heart-like commissurals, the remainder being much reduced, and decreasing in size anteriorly; commissurals in X–XIII have thin connectives to both the dorsal and supra-oesophageal vessels; the latter is visible in segments X–XVI only, though ill-defined in segments X and XI. Gizzard very large, cylindrical and highly muscular, though somewhat compressible, in V. Oesophagus narrow, with conspicuous lateral pouching in XIV–XVI (in PI only present in XIV and XV); these outpouchings are internally lamellate, but their function is conjectural (calciferous, digestive, etc.); a further small dilatation of the oesophagus is present in XIII. Intestine commences with abrupt expansion in XVII or XVIII, a definite double-ridged dorsal typhlosole present from XIX posteriad, being maximally developed from segment XXX. Nephridial system meronephric, in the forebody consisting of numerous, simple astomate,

exonephric loops in each segment (more than 30 in the intestinal region); Caudally (i.e. the last 35–40 segments), the nephridial bodies of the last 15 or so segments being considerably enlarged. No enteronephry demonstrable; tufting present in IV, presumably enteronephric, but the composite ducts not traceable; the nephridial loops noticeably longer in V and the following oesophageal segments than in the intestinal region. Holandric; 2 pairs small, highly convolute non-iridescent sperm funnels in X and XI, the former the larger; 2 pairs rounded, racemose seminal vesicles in XI and XII, the latter being obviously the larger; (or vice versa). Vasa deferentia readily traceable on the body wall as a pair of closely associated tortuous tubes entering the parietes in XVII. Prostates, 2 pairs in XVII and XIX, each a narrow, highly coiled tube, restricted to its segment of origin, with a long, thick, looped muscular duct; the anterior prostates are invariably the larger pair. Medium-sized penisetal follicles, containing few reserve setae, present in XVII and XIX, associated with the prostatic ducts; extensive copulatory musculature present (i.e. connective ligaturing of the follicles to the body wall, for the eversion and/or retraction of the penial setae during copulation). The setae robust, stout, somewhat flattened, the ectal end often twisted, the tip invariably recurved; the ectal  $\frac{1}{3}$  is ornamented with incomplete, staggered circlets of short, irregular toothlets. Length of mature seta 0.88 mm; midshaft diameter  $31.7\text{ }\mu\text{m}$  (mean of 3). Ovaries fan-shaped, consisting of many strings of small oocytes, and these, together with medium-large oviducal funnels, are located in XIII. Spermathecae 2 pairs, in VIII and IX, each comprising a sacciform ampulla that is produced into a long digitiform projection (directed anteriorly in situ), and a sessile, U-shaped diverticulum studded with large, iridescent, intramural sperm chambers; the diverticulum is embedded in the wall of the sac-like portion of the ampulla; length of right spermatheca of IX 2.9 mm. Brain crescentic, with broad fusion of the supra-oesophageal ganglion; 2 quite distinct prostomial nerves arise close together at the point where the commissure widens to form the dorsal ganglion; these innervate different regions of the prostomium. Peristomial nerve single, but branching a short distance from its point of origin at the commissure (approximately midway between the sub- and supra-oesophageal ganglionic masses). Spermathecal genital setae absent; slightly enlarged setae



**Fig. 159.** *Neodiploptrema mcdonaldii* Jamieson, 1997, genital field of Holotype. [From Jamieson 1997]

are associated with the genital marking on left IX, but these are not specialised, and appear to be non-functional.

### Remarks

*Neodiploptrema lacisbrontoii* is distinguished from other members of the genus in lacking genital setae, in having the male pores in an anterior position (near 17/18), and in exhibiting oesophageal pouching in the region XIV–XVI. Its closest affinities appear to lie with the much larger *Neodiploptrema raveni*, though this relationship is by no means close (Dyne 1997).

### *Neodiploptrema mcdonaldi* Jamieson, 1997

(Figs 159–161)

*Neodiploptrema mcdonaldi* Jamieson, 1997: 249–251, Figs 17–19, 39.

**TYPE LOCALITY:** Qld, 13°44'17"S 143°20'15"E, Peach Creek, McIlraith Range, alt. 500–520 m, in creek bank, in pig diggings and/or in moist upper root horizon, notophyll vine forest with fan and feather palms, on Kintore adamallite granite. Coll. K.R. McDonald, A.J. Stewart, 23 Sept 1996.

**HOLOTYPE:** QM G212005.

**PARATYPES:** P1–4 QM G212006–212009; P5 QM G212010 (includes microscope slide of left posterior penial setae); P6 and 7 QM G212011–212012; P8 QM 212013; P9–12 QM G212014–17; 13 QM G212018.

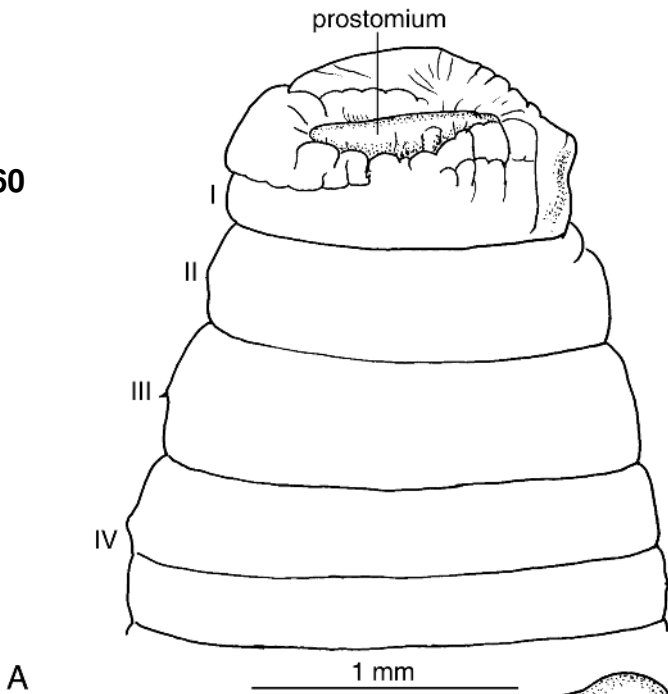
### Description (after Jamieson 1997)

Length 91–134 mm. Width (midclitellar) 4.6–50 mm. Segments 139–264. Circular in cross-section throughout. Pigmentless pale brownish grey in ethanol. Prostomium more than half the width of the peristomium; prolobous; first dorsal pore in 10/11 or 12/13; peristomium shorter than segment II. Setae 8 per segment, commencing on II, in XII, aa: ab: bc: cd: dd = 8.3: 1.0: 9.5: 1.2: 22.6; or 15.2: 1.8: 17.5: 2.3: 41.6%. Ventral setal couples absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital setae not demonstrable. Nephropores not recognisable. Clitellum well developed, saddle-shaped, extending over XIII–XIX, with a mid-ventral gap that extends to, or slightly lateral of, ab lines. Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a strongly protuberant oval papilla which is equatorial in line with the ventral setal couples (*ab*) relative to adjacent segments; the papillae of a side linked by a clearly developed narrow seminal groove which is bent medianwards (not forming parentheses) and is transversely incised by intersegmental furrows 17.18 and 18/19 and an intrasegmental groove of XVIII; the entire

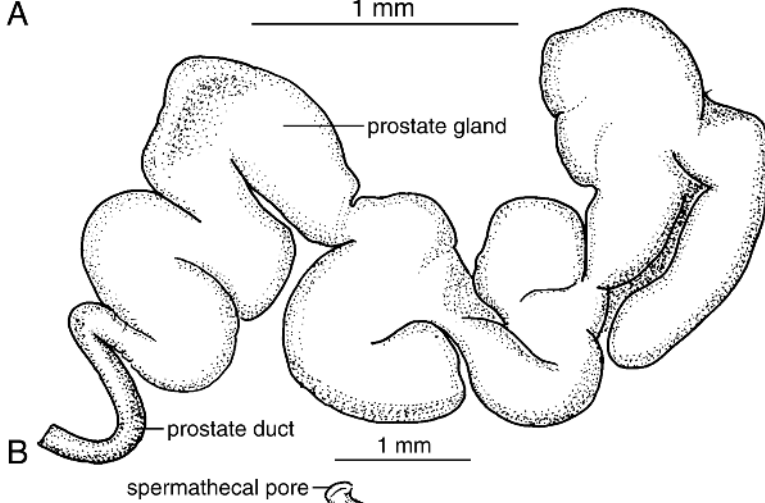
male genital area wider than long and not depressed. Genital markings: a broad, unpaired midventral pad extending laterally well beyond b lines, intersegmental in 10/11 and 14/15 and 21/22 but extending almost to the setal arcs of each adjacent segment; each pad traversed by a groove corresponding with the intersegmental furrow. Further markings a suggestion of a small papillae posteromedian to the prostatic porophores of XVII. Genital tumescences absent. Female pores, with elliptical borders, a pair near the anterior margin of XIV, in *ab*. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or slightly lateral of setae *b*; each on a conspicuous elliptical papilla which is wider than a setal couple.

Septa 6/7–9/10 strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in XI–XIII large, with conspicuous supra-oesophageal and smaller dorsal connectives; those in X slender, though still apparently latero-oesophageal; in IX anteriorly slender, with dorsal connective only. Gizzard moderately large and firmly muscular, in V, widening anteriorly. Oesophagus with a pair of lateral blood red dilations, with many closely situated circumferential vascular striae which correspond with low internal lamellae, in each of ½XII–XV; not pinched off from the oesophagus but true, sessile, calciferous glands as indicated by white granular contents which effervesce vigorously in dilute acid whereas the contents of the adjacent oesophagus and the intestine do not. Intestine commencing in XVII; a very deep bilaminar typhlosole commencing in XX. No anterior tufted nephridia present. At least four micromeronephridia on each side in the intestinal region; no funnels seen. Caudally with three or four meronephridia on each side, of which at least the median one has a preseptal funnel. Holandric; large seminal funnels with spermatozoal iridescence in X and XI. Large racemose seminal vesicles a pair in each of XI and XII, each vesicle a compact mass, with a single connection to the anterior septum of its segment, divided into many small iridescent loculi. Dendritic ovaries with many egg strings in XIV. Prostate glands flattened very tortuous wide tubes investing the intestine, a pair in each of XVII and XIX; with a narrow S-shaped duct the ental fourth of which is transitional to the structure of the gland. Penisetal follicles immensely long and conspicuous, the posterior pair extending posterolaterally to join the body wall in XXIV. Penial setae exceedingly thin and filiform; a long ectal region ornamented with many long slender sinuous scales directed obliquely towards the tip and standing well up from the surface; each scale itself consisting of three or more parallel pointed

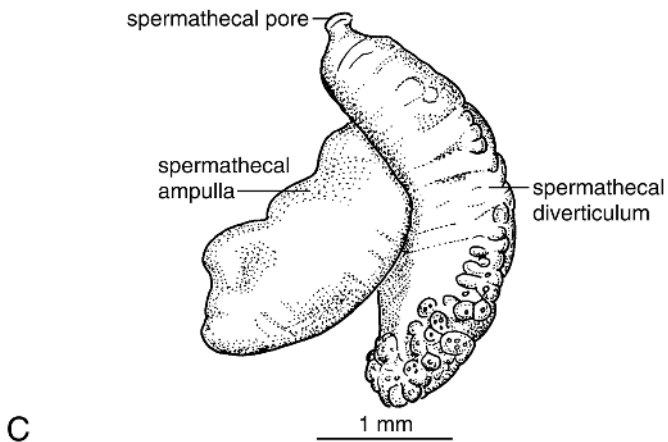
160



A



B



C

strands; length of a well-developed right posterior penial seta (straightened) = 6.7 mm. Genital setae not demonstrable. Spermathecae two pairs, in VIII and IX, the diverticulum (so identified by presence of sperm chambers) a tongue-shaped mass so large as to be visible on opening the specimen dorsally, resembling a seminal vesicle, its outer and terminal aspect with numerous small protuberant chambers containing sperm balls; the ampulla a slightly smaller pointed sac appearing to be an appendage of the diverticulum; the duct a short narrow ectal continuation from the diverticulum. Length right spermatheca of IX, from pore to tip of diverticulum = 3 mm; ratio length spermatheca: length duct = 17:1; length ampulla = 2 mm.

#### Remarks

*Neodiplotrema mcdonaldi* is distinguished from all other species of the genus by the large mammillated spermathecal diverticulum, which exceeds the length of the ampulla, and by the sinuous hair-like penial setae. A similar type of spermatheca occurs in *Diplotrema ridei* and, though less similar, in *D. shandi*. Close relationship of *N. mcdonaldi* to *D. ridei*, from Cape York and Melville Island, deserves consideration in view of considerable similarities of their genital fields.

#### *Neodiplotrema occidentalis* Dyne, 1997

(Figs 162, 163)

*Neodiplotrema occidentalis* Dyne, 1997: 146-147, figs 5, 11F.

**TYPE LOCALITY:** Qld, 12°35'S 141°55'E, Weipa, north bank of the Mission River, Cape York Peninsula, in semi-deciduous vine-forest, litter layer 4-5 cm deep, over black 'bauxite' soil. Coll. R. Raven, 7 Feb 1975.

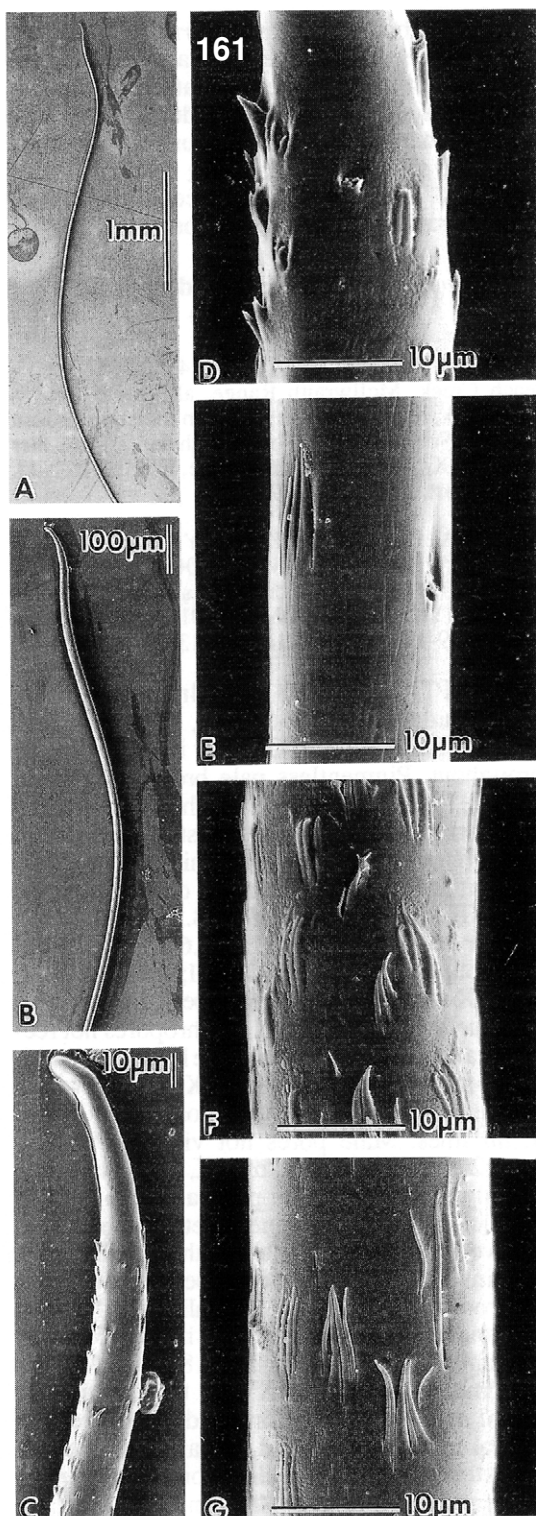
**HOLOTYPE:** GD 75/44.

**PARATYPES:** 2 acitellate specimens. GD 75/45.

#### Description (after Dyne 1997)

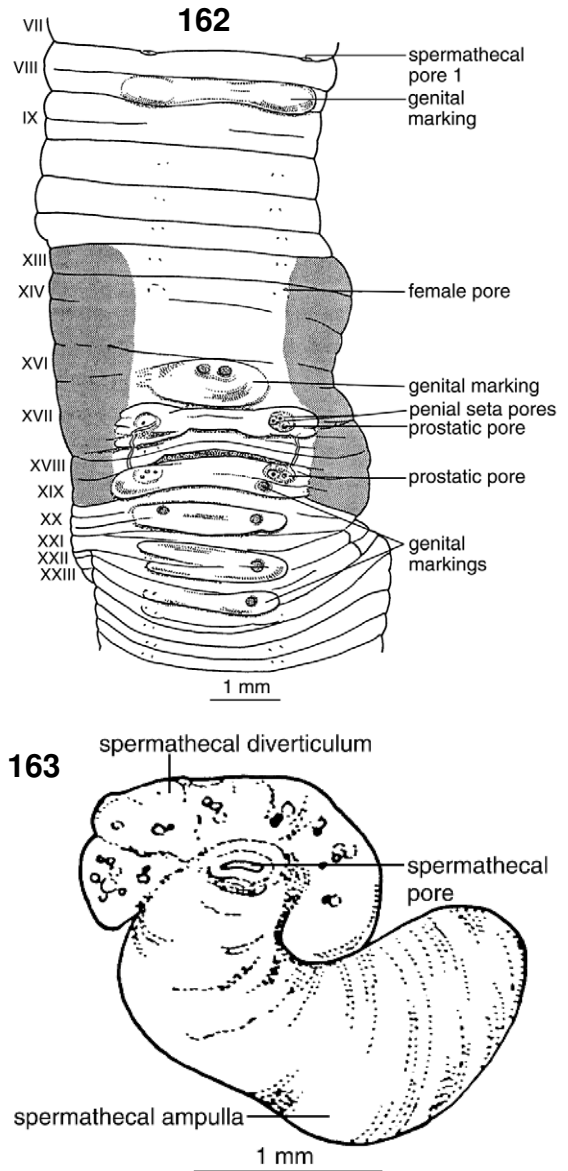
Length 59 mm. Width (midclitellar) 4.2-4.4 mm. Segments 135. Circular in cross-section throughout, pigmentless buff in ethanol. Prostomium propilobous, first dorsal pore 18/19. Setae 8 per segment, closely paired. Ventral setal couples of XVIII present; those of XVII and XIX enlarged as

**Figs 160, 161, *Neodiplotrema mcdonaldi* Jamieson, 1997, Holotype. 160, A, dorsal view in region of prostomium; B, right prostate of XVII, with penial setae omitted; C, right spermatheca of IX; 161, scanning electron micrographs of right penial seta of XIX: A, seta, excepting base; B, higher magnification; C-G, appearance of seta from tip to near the base. [From Jamieson 1997]**



penial setae; genital setae lacking. Nephropores not externally recognisable. Clitellum tumid, saddle-shaped, better developed dorsally, extending over segments XIII–XIX, the ventrolateral limits indefinite. Male pores not definitely demonstrable (owing to partial maceration), but presumed to lie within the shallow seminal grooves linking the prostatic pores of a side; the latter are atop tumid mounds that are connected across the ventrum by raised glandular strips. Each prostatic papilla bears 3 conspicuous pores: the two more closely associated openings marking the site of exit of the penial setae (as evidenced by the occasional protruding seta), whilst the remaining orifice is the prostatic opening proper. Female pores a pair of obvious slits close to seta b in XIV. Accessory markings a series of single, median pads with paired pore-like centres: a marking in XVI, with the oculate dimpling closely paired, in the setal arc; a set of markings decreasing in lateral width posteriad, commences in XIX, immediately posterior to the prostatic porophores (confluent with the tumid strip linking the latter), and extends to XXII, the eye-like margins widely spaced, not always present on the right side; a further slight swelling is present medially in XXIII. The small protuberances in VIII, which overhang the spermathecal pores are apparently not associated with genital seta follicles. Spermathecal pores inconspicuous in 7/8 and 8/9, aligned with ab.

Septa 5/6 diaphanous, 6/7 slightly thickened, 7/8–9/10 moderately thus, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, these commissurals being the only ones of any significant size, though those in XII are fairly robust; commissurals in XI–XIII demonstrably latero-oesophageal, with the supra-oesophageal vessel visible in segments X–XIII only. Gizzard large and firm, dolioform, in 5/6; oesophagus narrow, its length partially restricted by the posteriorly transgressive gizzard; intestine commences in XVI, no definite typhlosome noted. Meronephric throughout; a pair of very large tufts present III, their composite ducts running antieriad to discharge into the buccal cavity; in the mid-body, each segment possesses approximately 10/12 scattered astomate, exonephric loops; caudally, the medianmost nephridium is enlarged as a megameronephridium (on each side), having a large, preseptal nephrostome; its ducts were not traceable owing to poor fixation; the remaining nephridia are smaller, astomate, and reduced in number (apparently only 3 on each side, regularly spaced). Metandric; a single pair of faintly iridescent spermathecal funnels that are nonetheless quite large, together with presumed testicular tissue (attached to posterior face of septum 10/11),



**Figs 162, 163.** *Neodiploptrema occidentalis* Dyne, 1997, Holotype. **162**, genital field; **163**, right spermatheca of IX. [After Dyne 1997]

seen in XI; the funnels are situated on septum 11/12, above the ventral body wall, with the vasa deferentia running down the septum and onto the peritoneum, where they are traceable as single, lazily winding ducts. A single large pair of seminal vesicles that are finely racemose are located in XII. Prostate glands 2 pairs of very thin, flattened tubes, restricted to XVII and XIX, the anterior pair obviously the larger; the ducts are straight and



poorly muscularised. Large, conjoined penisetal follicles containing numerous reserve setae, are associated with the ectal portion of the prostate glands and their ducts; copulatory musculature is reduced to thin ligaments; the setae gently curving, tapering gradually to a rather blunt tip; the ectal extremity (approx.  $\frac{1}{5}$  ornamented with incomplete rows of very short, jagged toothlets, which become sparser proximally. Length of mature seta 1.63 mm; midshaft diameter 34.2  $\mu\text{m}$  (mean of 2). Ovaries small, with minute funnels, in XIII, ovisacs not seen. Spermathecae 2 subequal pairs, in VIII and IX, each consisting of a bent, tubular ampulla, and sessile, reniform diverticulum, with ?radially arranged intramural sperm chambers containing innumerable brightly iridescent flecks. Length right spermatheca of IX 1.2 mm (base of ampulla to pore).

#### Remarks

*N. occidentalis* shares its metandric condition only with *N. ambrosensis* but differs, inter alia, from the latter in having paired papillae on VIII, in (apparently) lacking genital setae, and in certain nephridial peculiarities.

It is not known whether this species is linked through intermediate populations to the Lockerbie and Iron Range endemics, or is an interpluvial isolate. Semi-deciduous notophyll vine-thickets are very restricted in the Weipa region, usually located on well-drained sites where freshwater aquifers are close to the surface; if *N. occidentalis* is an obligate closed forest inhabitant, its range must necessarily be strictly limited (Dyne 1997).

#### *Neodiploptrema paripunctata* Jamieson, 1997 (Figs 164–167)

*Neodiploptrema paripunctata* Jamieson, 1997: 251–253, figs 20–23, 39.

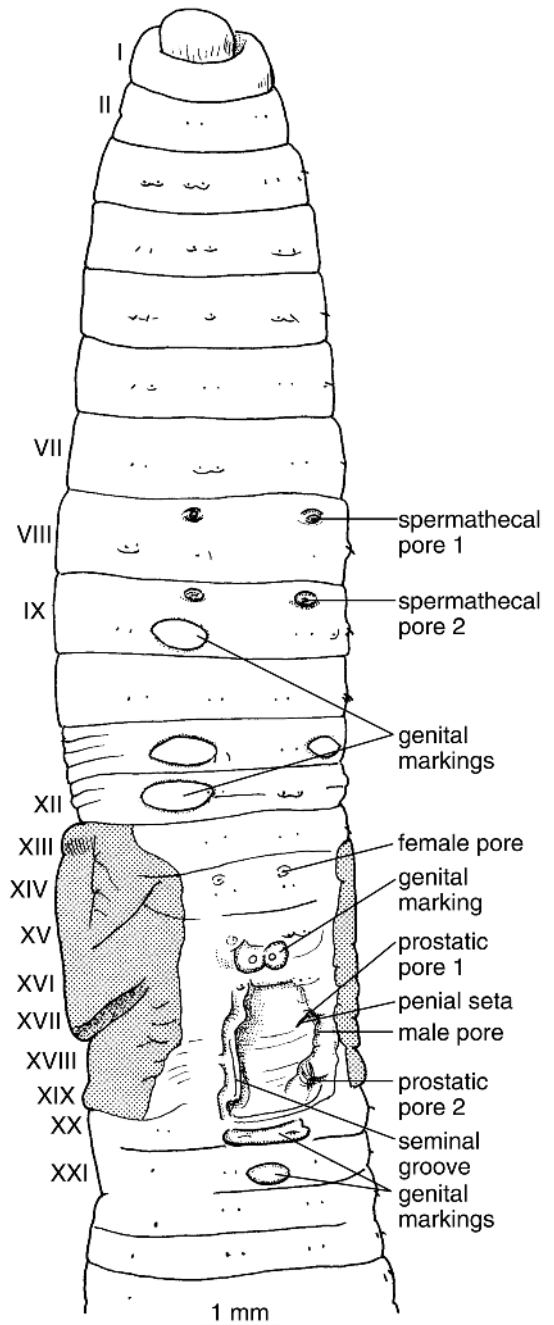
**TYPE LOCALITY:** Qld, 14°33.45'S 144°38.14'E, Altanmoui Section, Cape Melville National Park, altitude 520±10 m, in mesophyll vine forest, with feather palms, along creek, located from pig diggings. Coll. K. McDonald, P.J. Lethbridge, 7 and 10 Apr 1995.

**HOLOTYPE:** QM G213360.

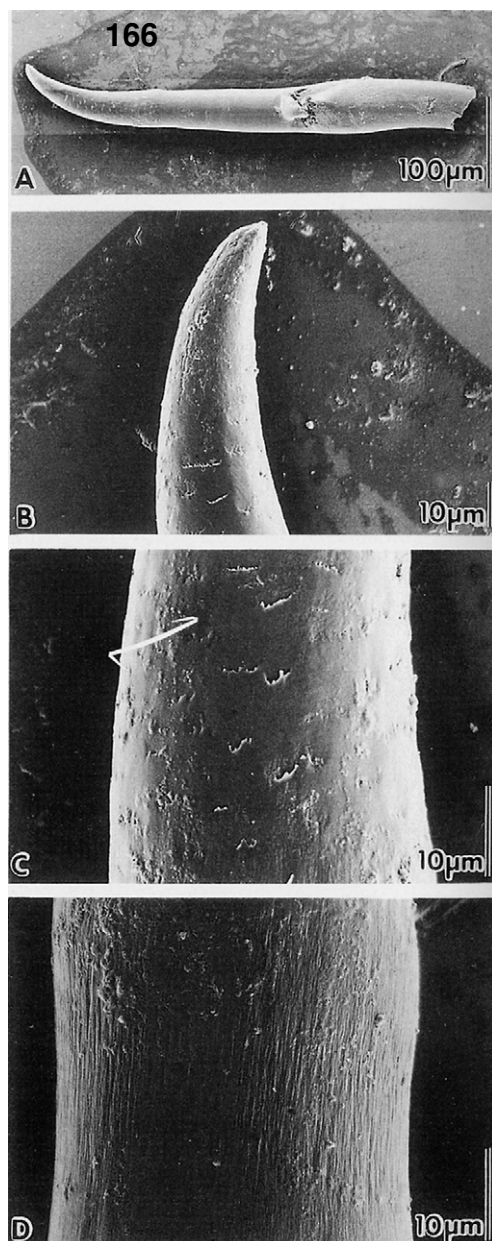
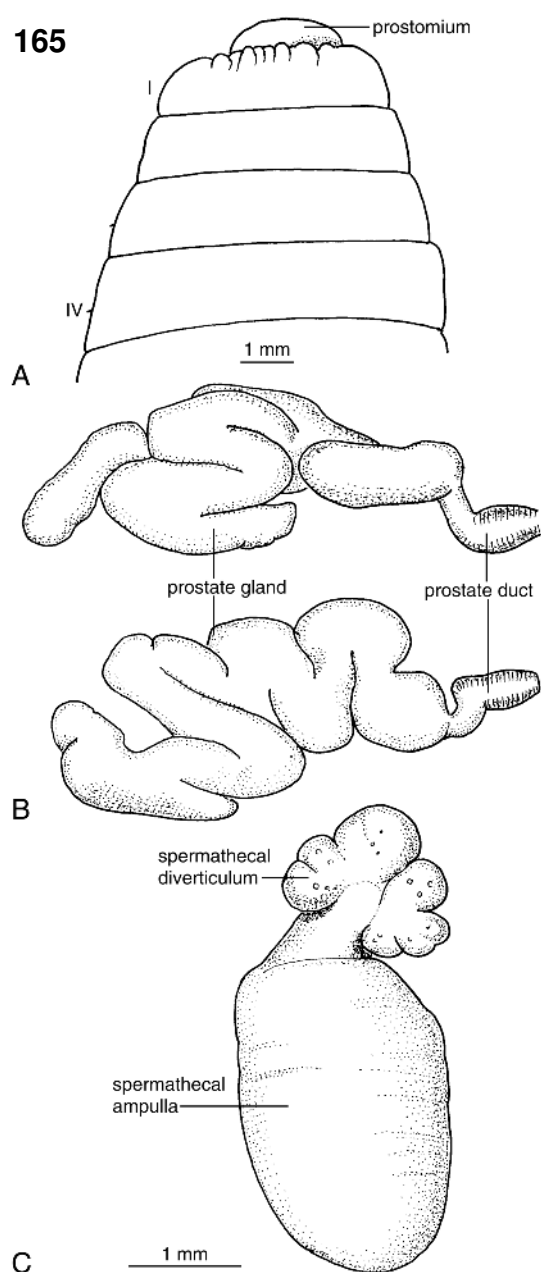
**PARATYPE:** P1 QM G213361.

#### Description (after Jamieson 1997)

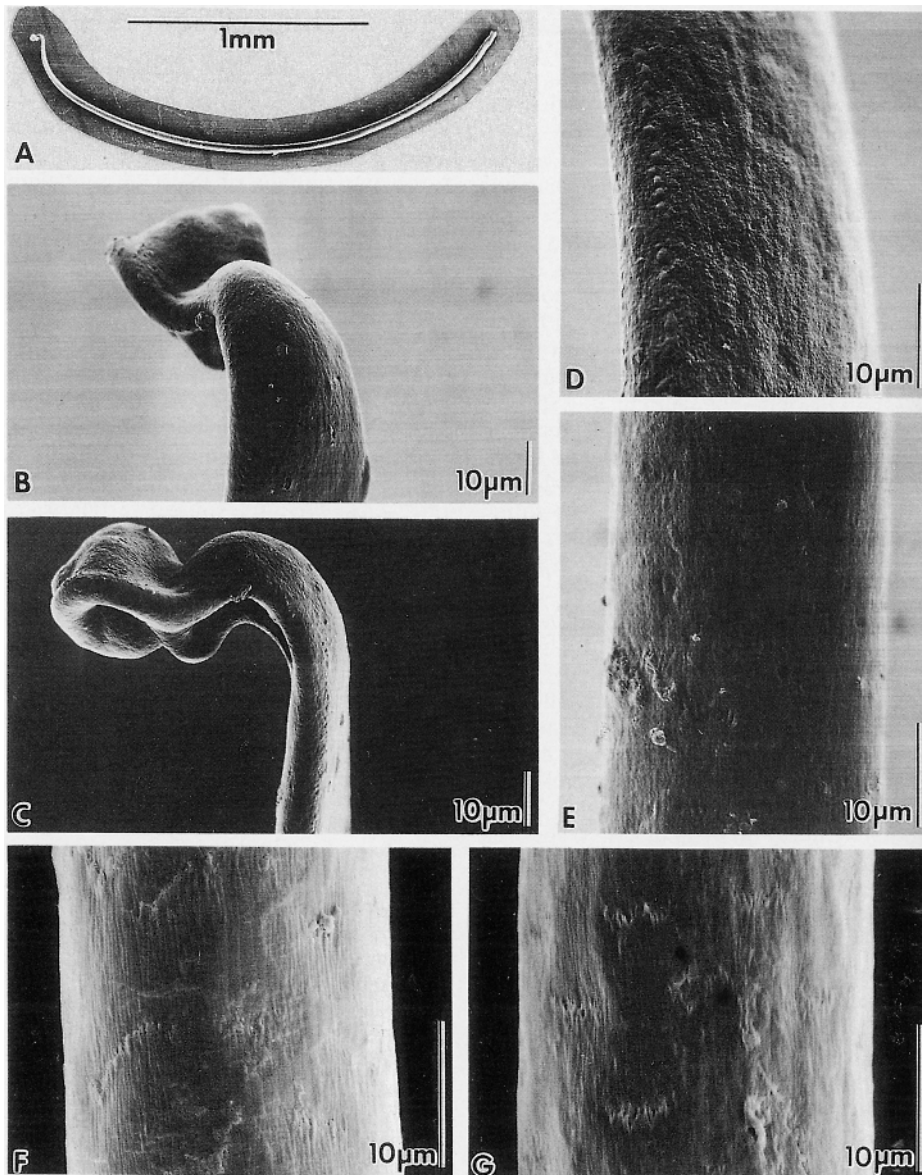
Length 150 mm. Width (midclitellar) 3.8 mm. Segments 171. Colour brown in ethanol with a pale grey-brown clitellum. Prostomium prolobous. Peristomium with anterior parallel grooves; approximately as long as segment II; not bisected ventrally. First open dorsal pore 18/19, but occluded pores present on the remaining, more



**Fig. 164.** *Neodiploptrema paripunctata* Jamieson, 1997, genital field of Holotype. [From Jamieson 1997]



**Figs 165, 166, *Neodiploptrema paripunctata* Jamieson, 1997, Holotype. 165, A, dorsal view of the region of the prostomium; B, left prostates, penial setae omitted; C, right spermatheca of IX; 166, scanning electron micrographs, ventral seta of VIII: A, seta, showing node typical of somatic seta; B-D, appearance of seta from tip to near base. [From Jamieson 1997]**



**Fig. 167.** *Neodiploptrema paripunctata* Jamieson, 1997, scanning electron micrographs of Holotype: **A**, left penial seta of XVII; **B-E**, appearance of the seta from the tip to near the base; **F, G**, ornamentation of left penial seta of XIX. [From Jamieson 1997]

anterior, segments of the clitellum. Setae 8 per segment, in regular longitudinal rows throughout; ventral setal couples of XVIII present immediately median to the seminal ridges; those of XVII and XIX modified as enlarged penial setae; genital setae absent; in XII, *aa: ab: bc: cd: dd* = 3.6: 1.0: 4.2: 1.0: 18.0; or 10.6: 2.9: 12.4: 2.9: 52.9%. Nephropores not visible. Clitellum saddle-shaped, protuberant, XIII–XIX; ventral margins well above *b* lines. Prostatic pores 2 pairs, in XVII and XIX, coincident with the protuberant penial setae, in line with the ventral setal couples (*ab*) of other segments; the pores on each side on small porophores which are not distinguished from a tumid parenthetic ridge which bears a simple seminal groove. A deep midventral depression present between the seminal grooves. Male pores a pair of minute orifices, on the seminal ridges, at the level of 17/18 and shortly lateral of *b* lines. Female pores in small oval fields anterior to the ventral setal couples (*ab*) of XIV. Spermathecal pores 2 pairs, a short distance posterior (relaxation artefact?) to 7/8 and 8/9, in *b* lines. Genital markings paired or unilateral pale non-protuberant oval patches, bordered by brown pigment, lateral of or just including setae *b*, in IX, XI and XII or also X; a pair of medially contiguous papillae midventrally in 15/16; a midventral transverse postsetal pad in XX; a small indistinct midventral oval pad in the posterior half of XXI in the holotype.

Septa 7/8–11/12 fairly strongly thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; those in X–XIII latero-oesophageal, with supra-oesophageal connective larger than the dorsal connective; commissurals in IX, and anteriorly, slender and with dorsal connectives only. Gizzard very large, cylindrical, slightly widening anteriorly, moderately firm and muscular, in VI(?), i.e. anterior to the diaphanous septum 6/7. Oesophagus lacking calciferous glands. Intestine commencing in XIX, not reaching full width until XXIV. A pair of moderate-sized, conical anterolateral diverticula on the intestine in XXVIII. No typhlosole found. Large tufted nephridia in II and IV send composite ducts to the wall of the buccal cavity and are accompanied laterally by many micromeronephridia; in the oesophageal region at least 12 micromeronephridia on each side, apparently all astomate and with no enlargement of the median pair; caudally with 8 meronephridia on each side, the medianmost one enlarged as a megameronephridium with a preseptal funnel; the lateral nephridia apparently lacking funnels. Holandric; iridescent seminal funnels in X and XI. Seminal vesicles in IX and XII; sacciform, those in IX subdivided into two or

more portions, and accompanied by a row of small vesicles; those in XII each forming an exceptionally large lobulated sac. Ovaries not detectable. Two subequal pairs of thickly tubular very tortuous prostates in XVII and XIX, limited to their segments, their surfaces minutely mammillated; the ectal duct with a stout, muscular ectal region and a shorter less muscular region, bent relative to this, which is narrow at its origin from the gland. Vasa deferentia not traceable. Penisetal follicles overlying the prostate ducts. Penial setae curved in an arc, the tip strongly recurved on itself or with a scroll-like expansion; ornamentation, on the shaft, consisting of weakly developed jagged transverse lines, each encircling less than one fourth of the circumference, and spaced longitudinally at approximately 10 µm intervals or these jagged lines very few and scarcely visible; length of a well-developed left penial seta of XVII = 2.5 mm; greatest width approximately 35 µm. Ventral setal couples of VIII and IX unmodified. Spermathecae two pairs, in VIII and IX; each with a large ovoid ampulla and a short narrower but poorly demarcated duct that is hidden except for its ectal end by a rosette-shaped multiloculate diverticulum which is incised slightly or deeply into approximately 8 large loculi in which many minute iridescent sperm balls are visible. Length of right spermatheca of IX = 8.2 mm; length ampulla = 2.9; ration of length spermatheca: length duct = 5.3; diameter of diverticulum 1.6 mm.

### Remarks

The pair of closely apposed genital markings in 15/16 is distinctive of *Neodiploptrema paripunctata*. This and the absence of large denticulations of the penial setae, is among features distinguishing it from the sympatric *N. altanmoui*. Intestinal diverticula are known in pheretimoids, in the Megascolecinae, but are exceptional in the Acanthodrilinae.

### *Neodiploptrema raveni* Dyne, 1997

(Figs 168, 169)

*Neodiploptrema raveni* Dyne, 1997: 147–149, figs 6, 11G.

**TYPE LOCALITY:** QLD, 1048'S 14228'E, Lockerbie East, Cape York Peninsula, collected through formalin expulsion of very rocky, red lateritic soil; Coll. R. Raven, 2 Feb 1975.

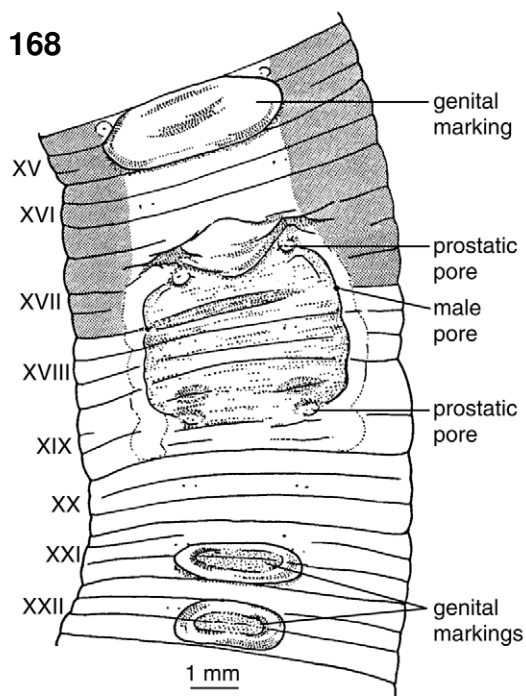
**HOLOTYPE:** QMGH 2951.

**PARATYPES:** Paratypes 1 and 3 QM G211959; paratypes 2 and 4, ANIC GD.95.9.4.

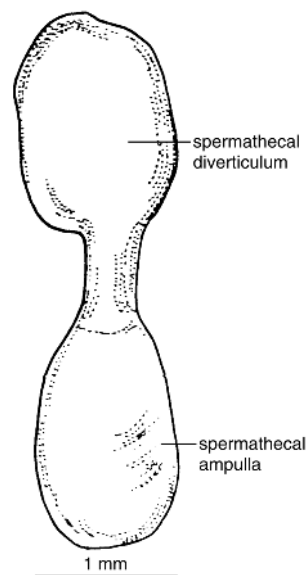
**Description (after Dyne 1997)**

Length 398–465 mm. Width (midclitellar) 9.0 mm. 6.8 mm. Segments 457–499. Circular in cross-section, pigmentless biscuit in alcohol. Prostomium pro-epilobous, peristomium much fissured. First dorsal pore 9/10 or 10/11. Setae 8 per segment, in regular longitudinal rows throughout; ventral seta couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of IX replaced by genital setae. Nephropores not seen. Clitellum saddle-shaped, weakly developed, over ½XII–XVII. Male pores inconspicuous, in the seminal grooves at 17/18, well lateral of *b* lines; prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices, on distinct mounds; the seminal grooves joining the pores of a side are very narrow, but deep, and are slightly convex laterally. The porophores lie in four distinctly sunken areas, which are transversely linked by two fairly broad channels, in XVII and XIX, the former of which is interrupted by a prominent cuneate tumescence in 16/17. The male genital area, bounded by the seminal grooves and the above-mentioned depressions, is concave with respect to the remainder of the body surface. Female pores inconspicuous openings well ventral of *a*, near 13/14. Spermathecal pores considerable, but located in deep intersegmental grooves, in 7/8 and 8/9, in *ab*. Accessory markings extensive torose tissue associated with the genital setae, in IX, forming a characteristic dumbbell-shaped tumid area (all specimens); a broad pad present in X, occasionally a similar marking in XI; a series of elliptical pad-like markings (extending across *bb*) with transversely depressed centres in all or some of XXI, XXII, and XXIII; a broad pad occupying much of the longitudinal dimension of XV, typically extends across *bb*.

Septa 5/6 moderately thickened, 6/7–10/11 much augmented with thick musculature (7/8–10/11 the strongest), 12/13 slightly thickened, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, only the commissurals in XI–XIII large, heart-like, and receiving connectives from both the dorsal and supra-oesophageal vessels. The latter connectives are the more substantial; the supra-oesophageal vessel was noted in segments X–XIII only. Gizzard, cylindrical, and virtually incompressible, in V; oesophagus completely suppressed by the posteriad encroachment of the gizzard in VI–X; thereafter highly vascular, but lacking pouching or calciferous glands. Intestine commences in XVIII, a strong dorsal typhlosole beginning abruptly at XIX. Meronephric throughout, nephridia commencing in II; very conspicuous, profusely divided tufts present in III and IV, their composite ducts



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**Figs 168, 169, *Neodiploptrema raveni* Dyne, 1997, Holotype. 168, genital field; 169, right spermatheca of IX. [After Dyne 1997]**

running anteriorly, but not traced. The oesophageal region with large numbers of astomate, exonephric, sessile loops restricted to the parietes or the septal bases; these are fewer in number in

the intestinal region, with a distinct concentration of bodies near the ventral nerve-cord; caudally, there is a multiplication and enlargement of the nephridial bodies, each apparently with its own preseptal nephrostome. Holandric; wispy testis material and small-medium spermatid funnels (diaphanous, translucent-?non-functional) present in X and XI, testis-sacs absent; large, acinous, very finely divided seminal vesicles present in XI and XII, the latter mass the larger. Prostate glands 2 pairs of simple tubular organs restricted to, and extending laterally in, their segments of origin; the anterior pair is the larger. Each gland possesses a fairly long, coiled, muscular duct. The *a* and *b* follicles of the penial setae are indistinguishable, forming 2 pairs of stout, strongly curved bundles joined to the body wall in a number of places by copulatory ligaments. The setae broad, flattened, attenuating abruptly near the ectal end, the ectal extremity invariably recurved; the shaft with a faint scattering of very fine clusters of short toothlets distally. Length of mature seta 3.43 mm; midshaft diameter 123.9  $\mu$ m (mean of 2). Medium-sized, pleated oviducal funnels seen in XIII, small ?ovisacs attached to the posterior face of septum 12/13. Spermathecae 2 pairs, in VIII and IX, each organ consisting of a rounded diverticulum sessile on the body wall (duct virtually non-existent), and a regular, ovoid ampulla connected to the latter by a distinct, narrow peduncle; length right spermatheca of IX 3.8 mm. Genital seta follicles a single pair, in IX, each containing several yellowish, slightly curved setae; these are ornamented over their ectal  $\frac{1}{3}$  not with scalloping, but with irregular transverse dentate grooves that are at the most  $\frac{1}{3}$  shaft circumference long. Length of mature seta 2.77 mm; midshaft diameter 79.5  $\mu$ m (mean of 3)

### Remarks

The lack of spermatozoal iridescence in the spermathecae or testis-segments in any of the specimens examined suggested a parthenogenetic mode of reproduction for the species. *N. raveni* is a very large, deep-burrowing, distinctive species which is very readily identified, even in a comparatively juvenile state, because of the peculiar bipartite spermathecae. It possibly also exists in the Torres Strait Islands in suitable habitats, but because of its burrowing habits, it would not be readily collected (Dyne 1997).

### *Neodiploptrema tumida* Dyne, 1997

(Figs 170–172)

*Neodiploptrema tumida* Dyne, 1997: 149–151, figs 7–8, 11E, H.

**TYPE LOCALITY:** QLD, ca 1048'S 142 28'E, Lockerbie East, Cape York Peninsula. Coll. R. Raven, Jan and Feb 1975.

**PARATYPE LOCALITIES:** 10°35'S 142°13'E, Green Hill, Thursday Island, in damp black clayey soil between rocks in vine-forest, paratypes 20–25. Coll. G. Berry, 7 Dec 1975.

**HOLOTYPE:** ANIC GD.95.9.8.

**PARATYPES:** P1, P3, P4, ANIC GD95.9.8; P5–6, ANIC GD95.9.6; P11–13 GD95.9.5; P14, ANIC GD.95.9.7; P10, P18 and P19 (desiccated) ANIC GD.95.9.9. (Paratypes 2, 15, 16, 17 not found.)

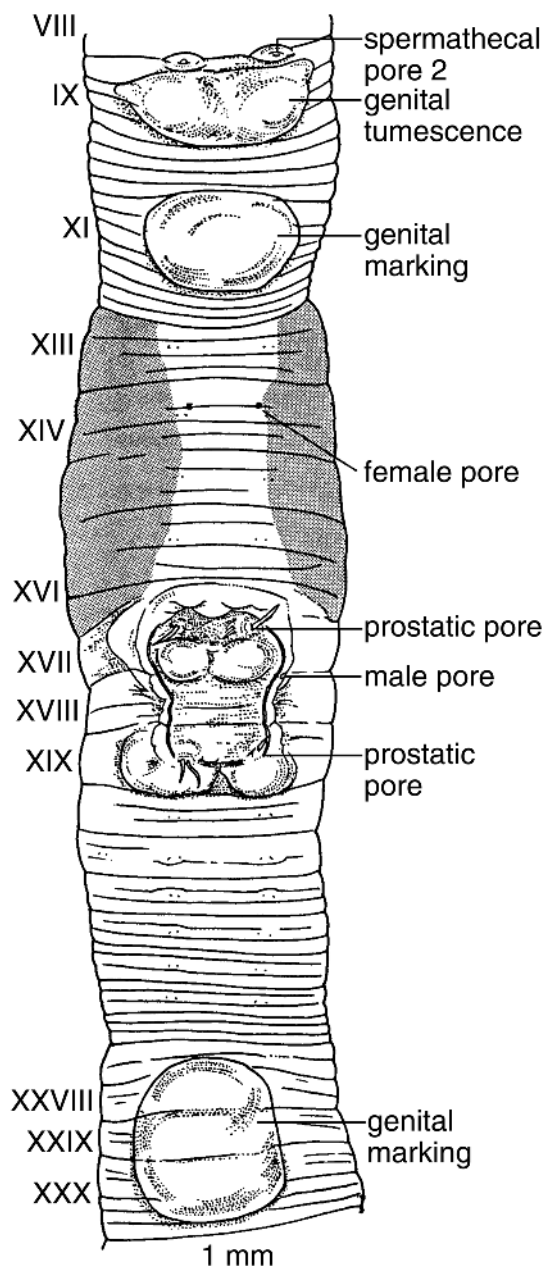
### Description (after Dyne 1997)

Length 142.5–149 mm. Width (midclitellar) 3.4–4.5 mm. Segments 242–282. Form circular in cross-section throughout, pigmentless buff in alcohol, clitellum in some specimens pink. Prostomium prolobous; first dorsal pore 8/9 or 9/10. Setae 8 per segment, in regular rows throughout; ventral setal couples of XVIII absent; those in XVII and XIX modified as penial setae; those of IX as genital setae. Nephropores not conspicuous. Clitellum strongly developed, saddle-shaped, over XIII–XVI; dorsal pores and intersegmental furrows distinct, setae obscured. Male pores slightly presetal, in narrow but deep seminal grooves that link the prostatic pores of a side; the latter are located in lateral depressions, separated by a central cuneiform tumescence; the posterior margins of the depressions in XVII and XIX are filled with 2 pairs of large, rounded swellings (anterior pair the larger), extending laterally to the seminal grooves, slightly beyond *b* lines; segment XVIII slightly raised and traversed by deep intrasegmental furrows, and longitudinally seminal grooves, which turn ventrally to *b* lines in XVIII. Female pores inconspicuous in a transverse furrow, just median of *a* lines near intersegment 13/14, in XIV. Accessory markings, a very large, swollen mound filling segment XI between the intersegmental furrows, and extending laterally beyond *b* lines by a distance approximately equal to *2bc* (all specimens); a similar tumescence extends over 3 segments (XXVIII–XXX), with some encroachment on segments XXVII and XXI; it is dissected by the intersegmental furrows of the segments it occupies; or only in XXVIII–XXIX; or XXIX–XXX; or rarely XXX–XXXI; a swollen mound associated with genital setae in IX, with similar proportions to the accessory markings in XI, or

markings in XXXII only; XXVIII–XXIX only; XXIX–XXX only; XXXI–½XXXII only; or XXIX–½XXXI only. Spermathecal pores very obvious on protuberant lips in *b* lines, in 7/8 and 8/9.

Septa 11/12 moderately, 6/7–10/11 strongly muscularised, 5/6 only slightly thickened. Dorsal blood vessel single, continuous onto pharynx, where it divides repeatedly in III and IV. Supra-oesophageal vessel present, ½XI–XIV. Last hearts in XIII; those in XI–XIII the largest, receiving connectives from dorsal and supra-oesophageal vessels, the latter sending the larger connectives in XII and XXIII; the remaining commissurals decreasing in size anteriorly, and dorso-ventral only. Gizzard large, highly muscular, and barrel-shaped, in V, with conspicuous midlength furrow. Oesophagus rather wide, thin-walled, in VI–XVI, vascularised to any extent only in XI–XVI; calciferous glands or pouching absent. Intestine commencing in XVII, with a low dorsal typhlosole commencing early, well developed by XXV. Meronephric throughout; the pre-intestinal region with scattered astomate exonephric loops adherent to the body wall and septa, becoming more numerous in the intestinal region posteriad of XV (here the nephridial bodies are attached exclusively to the body wall); caudally with slight enlargement of the nephridial bodies each with a conspicuous pre-septal nephrostome (at least 8 counted on each side); robust pharyngeal tufting present in III and IV, the composite ducts not traced.

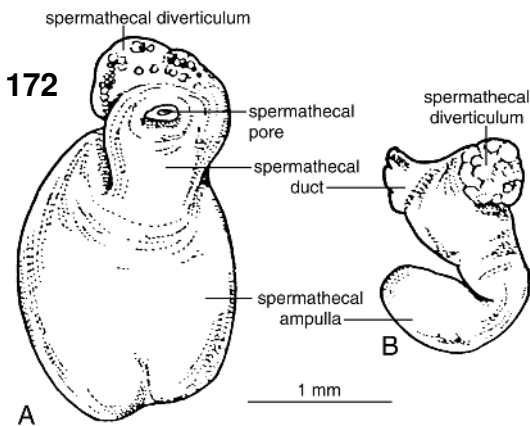
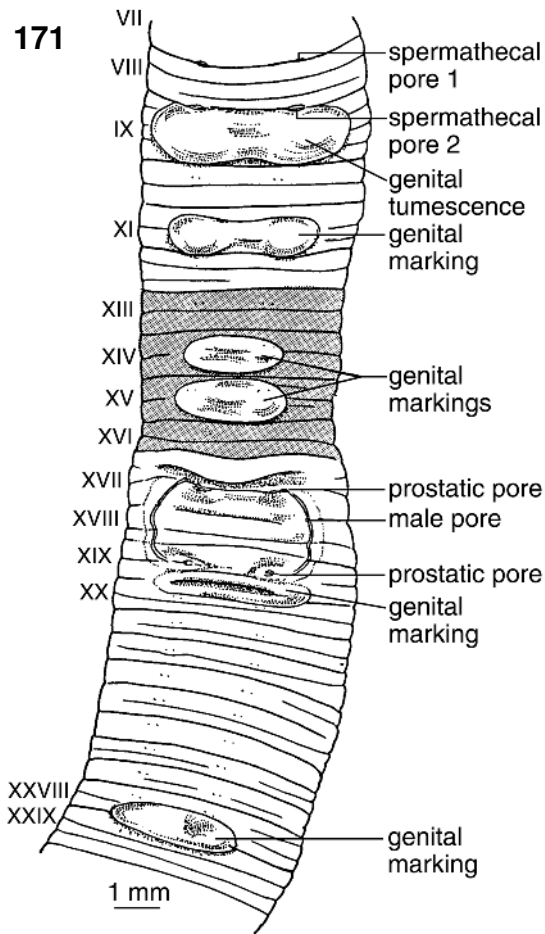
Holandric; small, iridescent, compactly plicate funnels and compacted sperm masses present in X and XI; loosely packed seminal vesicles with small, scattered loculi present in XI and XII. Prostate glands small, flattened, tightly coiled tubular organs with origins in XVII and XIX, the latter pair much reduced (?becoming vestigial); a very long, coiled, muscular duct enters a lobulate glandular mass on each side in XVII, but these enter the parietes directly in XIX. Penis setal follicles conspicuous, and attached by ligaments to the body wall in XVII, the bundles reduced in size in XIX; the setae are fairly long, and bent into an arc; the distal portion is often twisted with respect to the main axis of the seta, the extreme ectal tip is invariably sharply recurved, uniform, the immediately posteriad portion of the shaft obviously thickened; the ectal portion of the shaft is ornamented with short, discontinuous rows of fine teeth, the rows arranged in a crude alternation. Length of mature seta 2.29 mm; midshaft diameter 77.0 µm (mean of 2). Small ovaries, and medium-sized plicate funnels seen in XIII, ovisacs (?) attached to the posterior face of septum 12/13. Spermathecae 2 pairs in VIII and IX, the posterior



**Fig. 170.** *Neodiplotrema tumida* Dyne, 1997, genital field of Holotype. [After Dyne 1997]

pair readily perceived as the larger; each organ consists of a large, ovoid, bipartite ampulla, and a flattened, sessile, multi-loculate diverticulum occupying the dorsal aspect of the smaller ampullal portion; duct extremely short; length of right spermatheca of IX 2.7 mm. A pair of small

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**Figs 171, 172, *Neodiploptrema tumida* Dyne, 1997.**  
 171, genital field of Thursday Island, Paratype 20;  
 172, A, right spermatheca of IX, Holotype; B, right  
 spermatheca of IX, Thursday Island, Paratype 20.

[After Dyne 1997]

genital seta follicles present in IX (directed anteriorly, lying beneath the spermathecae); specialised glands lacking; the setae fairly straight, the ectal  $\frac{1}{5}$  distinctly ornamented with deep notching, the proximal rims of which are armed with irregular, sharp, triangular teeth. Length of mature seta 2.29 mm; midshaft diameter 52.4  $\mu$ m (mean of 3).

### Remarks

The Thursday Island specimens differ in a number of respects from the Lockerbie forms, almost to the extent that subspecific rank might be warranted. There are, however, unusual morphological features common to both that signify close relationship. The major divergences from the type description exhibited by the Thursday Island forms are as follows: length 140–175 mm; width (midclitellar) 4.4–4.7 mm; segments 313–324; first dorsal pore 9/10–11/12. Accessory markings a large, tumid pad extending across cc, and filling segment IX longitudinally; a pair of mounds or composite bipartite tumescences post-setally in XI, extending laterally to mid-bc or also XV; a large, median tumid pad occupying most of segment XXVIII and the extreme anterior portion of XXIX. Supra-oesophageal vessel seen in X–XVI; intestine commences in XIX; typhlosome commences immediately, but enlarges abruptly in XXXI as a complex, 4-folded structure; posterior prostate glands not much reduced (as for mainland specimens); spermathecal ampulla bent, slightly bulbous ectally, the diverticulum a sessile tubercle on the bulbous portion of the ampulla. Length right spermatheca of IX (base of ampulla to pore 2.6 mm).

The presence of genital setae in IX, the location of the male pores in 17/18, the occurrence of a large genital pad in the vicinity of XXVIII–XXXI, and the terminally bulbous, hooked penial setae are all characteristic of *N. tumida*, and may be used in combination to confirm identity. Immature material from Horn Island may also be referable to this species, a further indication that it is comparatively widespread. Little divergence has apparently occurred since the presumed separation of the mainland from Thursday Island populations after the drowning of Torres Strait, approximately 6,500–8,000 years BP. The duration of insular isolation is approximately equivalent to that experienced by mainland and Melville Island populations of *Diploptrema ridei* in the Northern Territory, though overall morphological divergence is slightly more pronounced in the latter case (Dyne 1997).

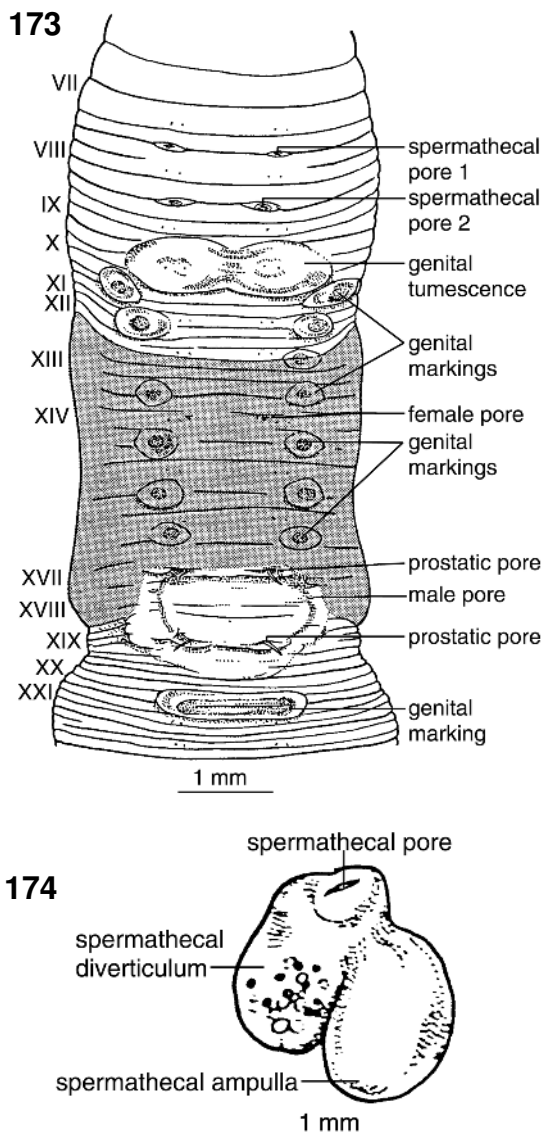


***Neodiploptrema varionephrica* Dyne, 1997**

(Figs 173, 174)

*Neodiploptrema varionephrica* Dyne, 1997: 151–153, fig. 9.**TYPE LOCALITY:** Qld, 10°46'S 142°34'E, E side of Lake Bronto, approximately 10 km from the tip of Cape York Peninsula, in dark sandy soil in open *Eucalyptus* dominated forest, with dense ground cover. Coll. R. Raven, 2 Feb 1975.**HOLOTYPE:** QMGH 2952.**PARATYPES:** QMGH 2953.**FURTHER MATERIAL:** Qld, Lake Bronto, on eastern side of lake, open eucalypt forest, much ground cover, dark sandy soil. One specimen registered as QMG 211960; 11 further specimens registered as QMG 211961.**Description (after Dyne 1997)**

Length 43 mm. Width (midclitellar) 3.0–3.1 mm. Segments 155, 110. Form circular in cross-section throughout, pigmentless grey-buff in alcohol, clitellum a slight pinkish-brown. First dorsal pore 11/12, prostomium pro-epilobous. Setae 8 per segment, commencing in II, in regular longitudinal rows throughout; ventral couples of XVIII absent or much reduced; those of XVII and XIX modified as enlarged penial setae; those of X replaced by genital setae. Nephropores not visible externally. Clitellum annular, more pronounced dorsally, over XIII–XVIII; dorsal pores obscured, intersegmental furrows only visible ventrally. Male pores small slits located in the relatively broad seminal grooves linking the porophores of a side; the male openings are well lateral of *b* lines, located approximately midway between the setal arc and 17/18; prostatic pores 2 pairs, in XVII and XIX, each on a slight protuberance overhanging a deep transverse fissure. Female pores small slits barely presetal, median of *a* lines by the distance *ab*. Spermathecal pores in 7/8 and 8/9, in *a* lines, the slit-like pores inclined at a slight angle to the plane of the intersegmental furrows. Accessory markings a conspicuous tumescence associated with the genital setae paired or unilateral in X. A series of up to 6 pairs of (sometimes unilateral) ellipsoidal intersegmental markings with oculate centres commencing in some or all of 10/11, in 11/12, in 12/13, in 13/14, in 14/15, in 15/16 and in 16/17. A broader tumid pad typically extends laterally to *b* lines to fill segment XIV between the intersegmental markings at 13/14 and 14/15; a similar transverse marking may be present in XX (to *b* lines); a transversely elliptical pad in 21/22, extending laterally to slightly beyond *b* lines is



**Figs 173, 174, *Neodiploptrema varionephrica* Dyne, 1997, Holotype. 173, genital field; 174, right spermatheca of IX.**  
[After Dyne 1997]

often present, with a similar marking less commonly occurring in 22/23; exceptionally, there is an additional marking similar to those in the clitellar region in 20/21. Genital seta location variations: located in some of VII (unilateral left), VIII, and IX (unilateral). In some specimens no accessory markings corresponding to genital seta locations were detected.

No septa strongly muscularised, but 6/7–10/11 slightly thicker than the remainder. Dorsal blood vessel single; last hearts in XIII, those in X–XIII with thin connectives received from the dorsal and supra-oesophageal vessels; the latter vessel is detectable in IX–XIII. Gizzard large, well developed, though compressible, in V, with a softer proventricular portion; oesophagus fairly short, somewhat compressed due to the posterior transgression of the gizzard (septum to 12/13 directed posteriad as a result of the latter); oesophagus well vascularised, with conspicuous rugae on its inner walls; 3 pairs of large, lateral outpouchings present in XVI–XVIII, containing definite lamellae, but all interconnected, with a single narrow opening leading to the oesophagus proper in XVII. Intestinal origin at posterior end of XVIII, a strongly developed dorsal typhlosole commencing in XXIV. Meronephric; large tufts developed in V, their composite ducts passing anteriorly to the buccal cavity; smaller clusters of loops seen in IV and ?III; the oesophageal region with approximately 6 small astomate, exonephric loops on each side; in segment XX, a conspicuous megameronephridium developed on each side, with a large preseptal nephrostome, and long excretory duct discharging into a thin-walled ureter running the length of the body on either side of the ventral nerve-cord, in *ab*; in addition, 3 small micromeronephridial loops are retained on each side of a segment: one in *bc*, with minute ducts entering the parietes in *b* lines, an intermediate lateral loop above *d*, and a dorsal body close to the middorsal line (the latter are all astomate and exonephric); this arrangement persists to the extreme caudal segments, the ureters apparently discharging at the anus; the megameronephridia are lost some 30 segments from the posterior end.

Holandric; compacted sperm masses and medium-sized iridescent funnels seen in X and XI; 2 pairs of seminal vesicles, consisting of large, loosely associated loculi, present in IX and XII, the posterior set much larger. Prostate glands 2 pairs of relatively small, simple tubular structures with short, muscular ducts, restricted to XVII and XIX; penisetal follicles rather small, but densely packed with reserve setae; a single band-like ligature passes across the prostates to link the follicles to the body wall near the mid-dorsal line. The setae gently curving, the tip invariably with a very distinctive trilobate appearance, the ectal  $\frac{1}{4}$  of the shaft bearing an irregular scattering of thorn-like (slightly recurved) spines. Length of mature seta 1.04 mm; midshaft diameter 44.3  $\mu\text{m}$  (mean of 3). Ovaries consist of flabelliform clusters of oocytes; these and medium-large oviducal funnels are present in XIII; no ovisacs seen. Spermathecae consisting of an ovoid ampulla and a short, blunt diverticulum containing a number of iridescent intramural pockets. Length right spermatheca of IX 1.2 mm. Genital seta follicles usually located in IX, no glandular structures associated; the follicles have some copulatory musculature; the setae are fairly straight, ornamented over the ectal  $\frac{1}{2}$ – $\frac{1}{3}$  with regular notching.

### Remarks

*Neodiploptrema varionephrica* is closely allied to *N. exigua*, the major synapomorphic character being the peculiar nephridial arrangement (mixed mega- and micromeronephridia in the mid-body, with ureters). *N. varionephrica* may be distinguished on the basis of its very distinctive penial setae, which, unlike any known Australian acanthodrilids, possess trifid tips. Other somatic characters, such as the position of the first intestinal segment, and the presence or absence of genital setae may also be used in conjunction with penial seta morphology to identify the species (Dyne 1997).

## ***Rhododrilus* Beddard, 1889**

*Rhododrilus* Beddard, 1889: 380.

**Type-species:** *Rhododrilus minutus* Beddard, 1889.

*Microscolex* (part.); Beddard 1895b: 459.

*Rhododrilus* + *Microscolex* (part.); Michaelsen 1900b: 143.

*Rhododrilus* + *Leptodrilus*: Pickford 1937: 89.

*Rhododrilus*; Lee 1959: 130; Jamieson 1971b: 103–105.

### **Diagnosis**

Setae 8 per segment. A pair of prostatic pores on XVII, combined with or separate from the male pores. Prostates tubular. Gizzard usually strongly developed. Holonephric, with or without bladders. Genital setae absent.

### **Description (after Beddard 1889; Jamieson 1971b)**

Small earthworms with less than 200 segments. Prostomium pro-epilobous to epilobous. Setae 8 per segment, closely paired. Clitellum occasionally not distinguishable; when present developed over 3 to 7 segments between XII and XVIII. Nephropores in a single series on each side of the body, from shortly below c to d. Prostatic pores 1 pair, on XVII (in one species on XVI) usually on papillae; male pores, if not combined with prostatic pores, 1 pair, usually on XVII close to prostatic pores, sometimes on anterior portion of XVIII, occasionally associated with posterior end of seminal grooves. Female pores 1 pair, on XIV, ventrolateral. Genital setae absent. Spermathecal pores 1–5 pairs, the last pair anterior to 9/10, ventrolateral.

Gizzard single, extending through 1 or 2 segments in the region of V–VIII, usually strongly developed, occasionally small. Calciferous glands present or absent. Dorsal blood vessel usually unpaired, occasionally paired for all or most of its length; 3 or 4 pairs of hearts, the last in XII or XIII. Holandric; testis-sacs absent. Penial setae usually present. Spermathecae usually each with 1 diverticulum, occasionally more than 1, diverticula sometimes projecting through the anterior septum into the next segment. Holonephric or

exceptionally (*R. disparatus*) with anterior meronephridia. Nephridial vesicles usually present, of various forms, sometimes absent.

### **Distribution**

New Zealand, Three-King Islands, Kermadec Is., Campbell Is., Auckland Is., Snares Is.; Tasmania.

### **Australian species (Peregrine)**

*Rhododrilus kermadecensis* Benham, 1905 (Tasmania and Kermadec Island).

### **Remarks**

Delineation of *Rhododrilus* from some other acanthodrilid genera is unsatisfactory and it is clearly a congeries. Of the 31 species, 29 are described by Lee (1959) from which source the generic definition, above, is largely derived. Lee (1962) validated *R. monticola* (Beddard) which in the earlier work he had considered *incertae sedis*. Lee has included in the genus *Leptodrilus* Benham, 1909, with male and prostatic pores in XVI. *Rhododrilus* is distinguished from the closely similar *Microscolex* principally in having a better-developed gizzard and in the closely paired setae, with no contraction of *ab* in the male genital region. It shows a wider variation of morphological characters than is common in other earthworm genera. The dendrogram of phenetic affinities of New Zealand genera given by Lee (1970) suggests that *Rhododrilus* is polyphyletic, the bulk of the species clustering with the type-species of *Microscolex*. Jamieson (1971b) found that attempted subdivision of *Rhododrilus* on the basis of discreteness of the male pores or their union with the prostatic pores, or on the numbers of pairs of spermathecae, bore little relationship to the geographical distribution of species.

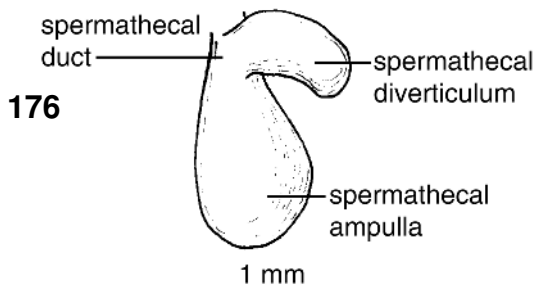
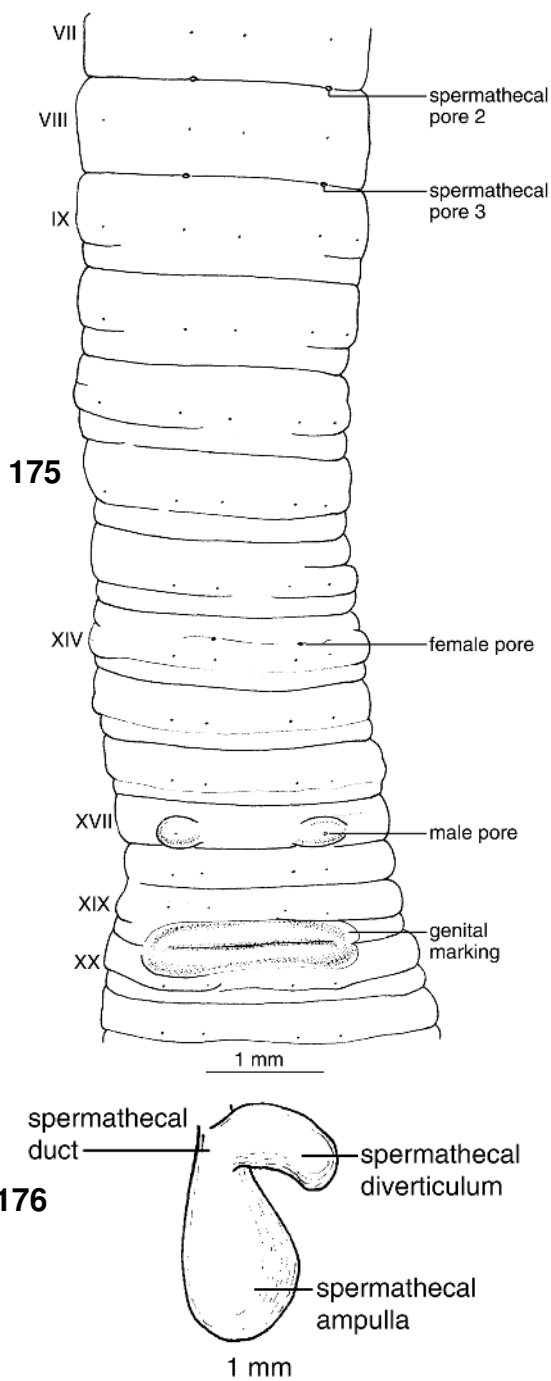
Dyne (1980) described a further species, *R. sexpapillatus*, from New Zealand. *R. queenslandicus* Michaelsen, 1916, was assigned to *Kayarmacia* by Jamieson (1997) and two additional species, *K. bursatus* and *K. cochlearis* are here transferred to *Kayarmacia*. Their anatomical affinities with the New Zealand *Rhododrilus* are minimal and it is here considered they represent an independent local derivation.

***Rhododrilus kermadecensis* Benham, 1905**

(Figs 175, 176)

*Rhododrilus kermadecensis* Benham, 1905: 299–300.*Rhododrilus kermadecensis*; Michaelsen 1907:142; Pickford 1937: 89; Lee 1952: 539; 1953: 49; 1959: 161–162, fig. 133–134; Blakemore 2000: 557.*Rhododrilus littoralis* Jamieson, 1974a: 213–216, fig. 4, 26C, 32E; pl. 60, table 1.**TYPE LOCALITY:** Kermadec Islands.**HOLOTYPE** of *R. kermadecensis*: Lost.**TYPE LOCALITY** of *R. littoralis*: Tas, ca 43°01'23"S 147°55'E Eagle Hawk Neck.**PARATYPE LOCALITIES** of *R. littoralis*: (1) As above. (2) Tas, Hobart and 'Strahan' [possibly Strahan, west coast of Tasmania?], 42°50'S 147°20'E.**HOLOTYPE** of *R. littoralis*: (1) TM K396.**PARATYPES** of *R. littoralis*: (1) BMNH 1973.2.53–54. TM K397–400. (2) AM W5339–5343; QM G213966.**Description (after Benham 1905; Jamieson 1974)**

Length 65–74 mm. Width 1.75–2.0 mm. Segments 103–108. Pinkish with transparent body wall. Prostomium epilobous, 1/2–2/3 peristomium, open, margins posteriorly convergent. Dorsal pores weakly developed behind the clitellum, possibly present as rudiments in the immediate preclitellar segments. Setal annuli strongly protuberant, excepting the anterior preclitellar and extreme caudal regions. Setae 8 per segment, commencing on II, in regular longitudinal rows throughout; setae a and b absent (replaced by penial setae) in XVII; in XII aa: ab: bc: cd: dd = 10.6: 6.2: 13.2: 12.2: 26.7; dd = 0.27 u (mean of two). Clitellum XIII, 1/3XIII–1/2XVIII, XVIII, saddle-shaped. Nephropores in c lines. A pair of rounded papillae on XVII, bears a pair of combined male and prostatic pores in b (Lee 1959, states that there are in posteriad order, the male pores, the prostatic pores and the pores of the penial setae, slightly median of setal lines b). Genital marking: a transverse pad in 19/20, extending laterally shortly beyond b lines, and longitudinally abutting on these setal annuli of XIX and XX; strongly tumid and may be transversely bisected by a furrow corresponding with but not peripherally continuous with furrow 19/20. Female pores on XIV, anteromedian of setae b or slightly lateral of a lines. Spermathecal pores minute, and may be visible with difficulty, 3 pairs, in 6/7, 7/8 and 8/9, in b or ab.



**Figs 175, 176.** *Rhododrilus kermadecensis* Benham, 1905 (Holotype of junior synonym, *R. littoralis* Jamieson, 1974, Dyne, 1984, unpublished). **175**, genital field; **176**, right spermatheca of IX. [After Jamieson 1974a]

Dorsal vessel single. Last hearts in XIII; those in X-XIII latero-oesophageal. Supra-oesophageal vessel in VIII?-XIV. Gizzard in V, small and easily compressible though muscular, or rudimentary. Oesophagus lacking calciferous glands but especially vascularised and with low internal rugae in VIII-XVI; and may be dilated in XIII and XIV. Intestine commencing in XVIII (Benham), dilating in XIX but possibly intestinal in XVII or XVIII? (Jamieson). Testes and funnels free in X and XI. Seminal vesicles in IX, XI and XII, racemose, increasing in size posteriad. Ovaries, with many egg-strings, in XIII. Ovisacs in XIV. Prostates one pair, in XVII-XXII, XXIII, long, very slenderly tubular, almost straight. Penisetae follicles very conspicuous, almost as wide as the prostates, and almost as extensive, extending through XVII-XXI, XXII; penial setae long, delicate, sinuous, curved distally, with shallowly spoon-shaped tip which may be recurved; length 2.8=3.7 mm, general width of shaft 11  $\mu$ m. Spermathecae 3 pairs, in VII, VIII and IX; ampulla ovoid with short, muscular duct about half the width of the ampulla; long, cylindrical diverticulum curved in S-shape, dilated near its junction with the duct or (Jamieson 1974a) or diverticulum (when uninseminated, at least) digitiform, and the spermatheca almost sessile on the body wall .

### Remarks

As proposed by Dyne (1984, unpublished) and confirmed by Blakemore (2000), *Rhododrilus littoralis* Jamieson, 1974, appears to be a junior synonym of *R. kermadecensis* Benham, 1905, previously known from a single specimen collected in the Kermadec Is. The type of *kermadecensis* is apparently lost, but Benham's original description and illustrations are adequate for reasonably confident identification; the broad genital pad in 19/20 is diagnostic. *R. littoralis* is in many respects close to *R. cockaynei* Benham, 1905, a species which is very widespread in the subantarctic islands, where it is often encountered in the intertidal zone. Its euryhaline propensities make it an excellent candidate for trans-oceanic dispersal. *R. littoralis* Jamieson, 1974b, differs from *R. cockaynei* in having the last hearts in XIII, and in lacking 'oesophageal glands' in XIII, thus conforming in this and many details to the description of *R. kermadecensis*. Although *R. kermadecensis* is found in Tasmania, it is doubtfully to be considered an Australian native. The above account is taken from the summary of Lee (1959) and that of the junior synonym, *R. littoralis*, by Jamieson (1974a).

## *Torresiella* Dyne 1997

*Torresiella* Dyne, 1997: 153.

**Type-species:** *Torresiella singularis* Dyne, 1997. (Monotypic genus).

### Diagnosis (after Dyne 1997)

Setae 8 per segment, prostates a single pair in XIX; male pores a single pair combined with the latter, on XIX. Spermathecal pores a single pair, ventro-lateral, in 7/8. Wholly meronephric, with astomate exonephric nephridia throughout; tufting present in the pharyngeal region. Gizzard well developed, in V. Calciferous glands absent. Holandric, testis-sacs absent. Penial setae and genital setae present.

### Description

As for the type-species.

### Remarks

*Torresiella*, like *Neodiploptrema*, is meronephric. It appears to be related to the *Diploptrema-Neodiploptrema* assemblage. Balantin reduction (male pores migrating posteriorly to unite with a single pair of prostatic pores, in XIX), which distinguishes *Torresiella* from all other Australian acanthodrilids, is a much less common phenomenon than is the microscolecin transformation (male pores migrating forwards to unite with a single pair of prostatic pores, in XVII). The term derives from a meronephric West African species described by Michaelsen (1898) for which he erected a new genus, *Balanta*. This was on the basis of the combined male and prostatic pores being located on XIX, an arrangement that had not previously been recorded. Only two years later, in 'Das Tierreich', Michaelsen (1900b) suppressed *Balanta* in *Dichogaster*, as its only species, *B. ehrhardti*, had close apparent affinities to other members of that genus [including meronephry] despite the acanthodrilin male genital terminalia of *Dichogaster* (Dyne 1997).

Other balantin genera include *Balanteodrilus* (monotypic) recorded from Yucatan Caves by Pickford (1938), and *Sylvodrilus*, a New Zealand

taxon. Partial balantin reduction is known from *Udeina montanus*, and *Pickfordia hemibalantina* Omodeo, 1958; in these species, the posterior prostates are retained, but the male pore has not migrated, remaining in XVIII. In *Sylvodrilus*, the male pores have shifted to the posterior part of XVIII, and in *Balanteodrilus*, they are located in 18/19. The most advanced degree of transformation is thus to be found in *Torresiella*, in which the male and prostatic ducts are intimately associated (fused?) behind the combined pore. This condition is approached in *Dichogaster ehrhardti*.

Why the balantin condition should be so rare is not known. In acanthodrilid genera, there is a distinct tendency for the anterior prostate glands to be conspicuously larger than the posterior organs. Correspondingly, the anterior spermathecae are often smaller than those posterior. Again, there is no satisfactory explanation for these observations, but they do indicate a certain predisposition to the microscolecin reduction. Intermediate stages in reduction suggest that in both reductions, elimination of one of the prostatic sets is a gradual process. The migration of the terminal end of the vas deferens must be largely influenced by the differential effects of the two prostatic pairs. This is presumed to be an embryonic phenomenon, the relative size of the prostatic primordia having a deterministic effect on the length of the vas deferens and the positioning of the male pore (the 'balanced' effect of subequal prostatic sets resulting in an equatorial or slightly presetal position of the male pore, as is commonly the case). A gradualist interpretation, where the male pore migrates progressively over many generations owing to some external selective force, though difficult to accept, appears to be appropriate in this instance. In cases where the male pore fails to migrate despite elimination of either prostatic pair, stabilising selection or some other influence may be involved (Dyne 1997).

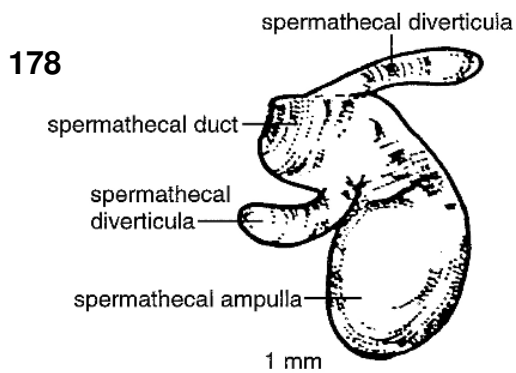
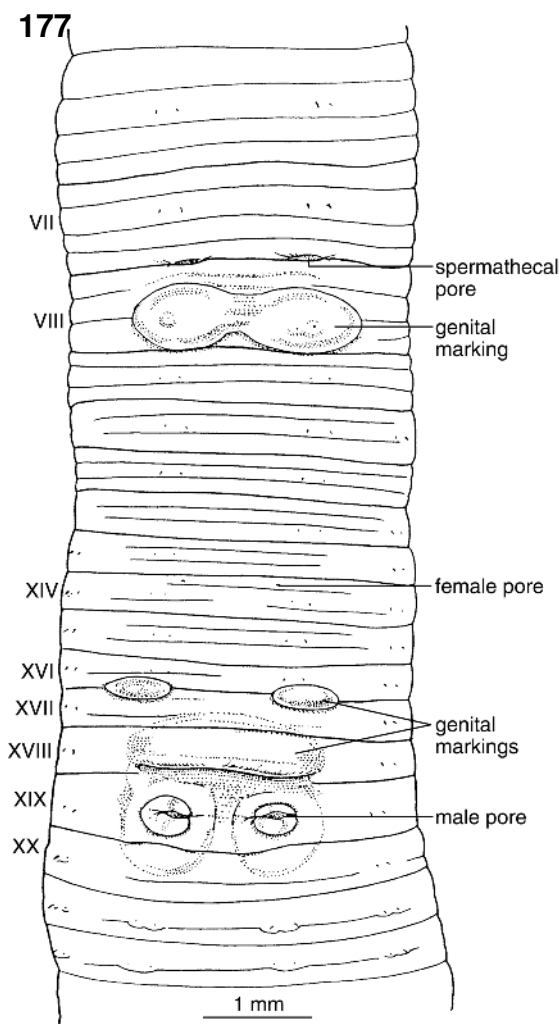
***Torresiella singularis* Dyne, 1997**

(Figs 177, 178)

*Torresiella singularis* Dyne, 1997: 153–155, figs 10, 11A.**TYPE LOCALITY:** Qld, 10°37'S 42°17'E, Horn Island, Torres Strait, 0.4 km E of the airstrip, in moist clay near eucalypts, beside a narrow creek. Coll. R. Raven, 27 Jan 1975.**HOLOTYPE:** QM GH 2936.**PARATYPE:** QM GH 2937.**Description (after Dyne 1997)**

Length 74–92 mm. Width (midclitellar) 3.3–3.4 mm. Segments ca 164–202. Uniformly circular in cross-section, pigmentless grey in alcohol. Prostomium prololobous, peristomium with a dorsal cleft. First dorsal pore 8/9. Setae 8 per segment, commencing in II; caudal setae conspicuously enlarged with respect to the other somatic setae; ventral setal couples of XIX modified as enlarged penial setae; those of XVII and XVIII lacking. Nephropores not externally recognisable. Clitellum not developed. Combined male and prostatic pores in *ab* on XIX, coincident with the penial seta orifices. The combined pores are located on low mounds, the anterior and posterior approaches of which have a darker, glandular appearance; the male field generally depresses, with a conspicuous furrow at 18/19, overhung anteriorly by a lightly tumid region across *bb*. Accessory markings slight tumid swelling associated with the development of genital setae usually present in VIII, below the spermathecal pores. Female pores minute points presetally, in an intrasegmental furrow, median of *a* lines, in XIV. Spermathecal pores a single pair, in *ab*, in 7/8, conspicuous as expanded, rimless orifices.

Septa 5/6 delicate, 6/7, 7/8, 8/9 with a slight to moderate thickening, 9/10–10/11 moderately muscularised, 11/12 slightly so. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X–XIII larger than the more anterior commissurals, and with connectives to both the dorsal and supra-oesophageal vessels (the remainder dorso-ventral only); supra-oesophageal vessel weakly developed, widest in XIV, not traceable anterior of VIII. Gizzard moderately large, muscular, dolioform, compressible, in V; oesophagus in VI–XVI, fairly wide, well supplied with blood vessels, dilating slightly intra-segmentally; expanded into broad outpouchings in XIII–XIV, not demarcated from the lumen, or calciferous gland-like. Intestine commences with gradual expansion in XVII, a strongly developed dorsal typhlosole present after XXV. Meronephric



**Figs 177, 178, *Torresiella singularis* Dyne, 1997.**  
**177**, genital field of Holotype; **178**, left spermatheca of Paratype 1.  
 [After Dyne 1997]

throughout; numerous, scattered, astomate, exonephric loops present on the parietes throughout, more numerous in the intestinal region. Caudally, with some slight increase in size, but with no evidence of nephrostomes or enteronephric development. A small tuft occurs in IV. Holandric; 2 pairs of small, slightly iridescent spermathecae in X and XI, with 2 pairs of small, loosely compacted seminal vesicles in IX and XII; vasa deferentia non-iridescent, clearly visible only in the 3 segments immediately preceding the prostatic segment; still paired on each side in XVIII, fusing in XIX, and entering the parietes simultaneously with the prostatic duct, ?fusing with the latter at this point. Prostate glands small organs, situated far laterally in XIX, extending into XX, with a few loose coils in the horizontal plane; the muscular duct of uniform diameter, long and straight, perhaps as long or longer than the uncoiled glandular portion, entering the parietes in XIX, through a glandular mass. Penial seta follicles conspicuous, *a* and *b* components distinguishable, each with only 2–3 yellowish setae; the follicles are attached to the body wall by a large band of retractor musculature passing across the prostate glands, and attached by

several strands in 20/21. The setae with a very straight shaft, ectally with a characteristic uncinate appearance; ornamentation restricted to a small region behind the point where the shaft begins to curve sharply, consisting of densely packed, short clusters of jagged teeth. Ovaries small, the ovarian funnels diaphanous, medium-sized, located in XIII; a pair of botryoidal ovisacs present, attached to the posterior face of septum 13/14. Genital seta follicles present in VIII, with attached musculature, but no glandular structures. The setae angular in cross-section, fairly straight, the ectal  $\frac{1}{2}$ – $\frac{1}{3}$  of the shaft conspicuously ornamented with dentate notching. Spermathecae a single pair, in VIII, each consisting of a pyriform ampulla, divided into 2 sections by a transverse constriction, and two discrete, clavate diverticula joining the ectal ampullar region; duct indistinguishable from the latter. Length of right spermatheca 2.1 mm (the diverticula sometimes terminally bifid).

#### Remarks

*T. singularis* is the only known balantin Australian acanthodril.



## ACKNOWLEDGEMENTS

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# Native Earthworms of Australia II

Earthworms contribute significantly to sustainability of our natural environment, and Australia has some remarkable forms. This review of the acanthodriline fauna completes the revision of Australia's known earthworms of the family Megascolecidae. A previous publication on the subfamily Megascolecinae by Barrie Jamieson, similarly made available on CD, was followed by a Supplement to that CD. We are now fortunate to have a review of Australia's acanthodriline earthworms (Megascolecidae), again presented in electronic form, and this time authored by Geoff Dyne and Barrie Jamieson. Here the Australian taxa are reviewed and new species and subspecies described.

A major aim of this work is to bring to light the manuscript species described by G.R. Dyne in a Ph.D. thesis (Dyne 1984), prepared under the supervision of the second author. The following genera are reviewed, and their known species and subspecies are described: *Diplotrema* Spencer, 1900; *Kayarmacia* Jamieson, 1997; *Microscolex* Rosa, 1887; *Neodiplotrema* Dyne, 1997; *Rhododrilus* Beddard, 1889; *Torresiella* Dyne, 1997. Keys to genera and species are given and 178 illustrations are included.

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